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Impact of soil compaction and organic matter removal on soil fauna in the Sub-Boreal Spruce zone of central British Columbia.

by

Jeffrey Paul Battigelli

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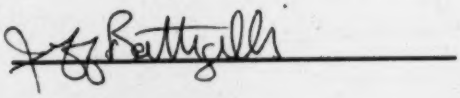

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Abstract

Soil fauna communities were compared among three sites in the Sub-Boreal Spruce biogeoclimatic zone of central British Columbia. The short-term impact of soil compaction and organic matter removal on the soil fauna community was also examined.

Densities of most faunal elements were highest in the organic horizon and increased from spring to fall. Densities of spiders were higher at Topley, Hymenoptera were highest at Skulow Lake and Chilopoda, Pseudoscorpionida and Lumbricidae were highest at Log Lake. Numerically, Acari represented 70-80% of the mesofauna and Collembola accounted for 15-20%. Relative abundance of Prostigmata was significantly higher and both density and relative abundance of Oribatida were significantly lower at Log Lake.

Eighty-nine oribatid mite species were identified, including 11 new species recorded for Canada and 45 new species for British Columbia. Only sixteen species were common to all three sites. Oppiella nova (Oudemanns) was numerically dominant at all sites and for all seasons. Oribatid species richness was higher in the organic horizon than in the mineral soil. Skulow Lake had more species than the other two sites. Furthermore, more species were unique to Skulow Lake than Log Lake or Topley. Species composition of the organic horizon was highly similar among sites. Species richness in the mineral soil did not differ among sites; however, the oribatid species assemblage in the mineral soil at Topley differed from those of the other two sites.

Densities of most taxa did not differ between uncut forest control plots and stem-only harvested plots. Whole tree harvest and forest floor removal combined with heavy soil compaction significantly reduced densities of soil fauna. Loss of forest floor represented a substantial loss of habitat for most soil fauna. The forest floor apparently limited the impact of soil compaction and fluctuations in soil temperature and moisture. Structure of the macrofauna community did not change with treatment severity. However, relative abundance of Prostigmata and Mesostigmata increased with treatment severity while that of Oribatida decreased. Oribatid mite diversity and species richness was significantly reduced with treatment severity. Furthermore, the number of rare oribatid species and evenness decreased as treatment severity increased. Oppiella nova and Suctobelbella sp.nr. acutidens were the dominant species in the forest floor and mineral soil, regardless of treatment.

To Graeme, Patrick and Charlotte

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Chapter 1: General Introduction

Soil has been described as our most precious non-renewable resource (Marshall et al. 1982) and is vital for productivity in terrestrial environments (Lavelle 1996). Chemical and physical properties of soils have been studied intensively for many years. Although soil organisms have a critical role in soil development (Pawluk 1985) and maintenance of soil fertility (Seastedt 1984), the biological component of soils has been largely ignored in North America. The abundance, diversity and ecological roles of soil animals in most North American forest soil ecosystems are poorly understood due to a lack of intensive studies and baseline information (Kevan 1985, Marshall 1993).

The opaque, three-dimensional nature of the soil environment makes studying these organisms difficult since they must be extracted from the soil (Ferris 1993). Furthermore, the great diversity and density of organisms in soil also impedes research. Species diversity of soil animals rivals that of a coral reef (Wallwork 1970). All major animal phyla are represented in the soil, except for Cnidaria, Ctenophora, Porifera and Echinodermata (Hole 1981). Hundreds of species, represented by thousands or millions of individuals, can occupy a single square meter of soil (Battigelli et al. 1994, Moldenke 1990). The soil ecosystem has been variously referred to as 'the poor-man's tropical rainforest' (Giller 1996, Usher et al. 1979) and 'the other last biotic frontier' (André et al. 1994).

Using body size, soil fauna can be classified into three groups: micro-, meso- and macrofauna (Swift et al. 1972). Microfauna, organisms <0.1mm wide,

include Protozoa, Nematoda, Tardigrada, Copepoda and Rotifera as well as the smallest forms of Acari. The majority of these organisms require water films around soil particles for habitat. Mesofauna range in size from 0.1 - 2 mm wide and include Acari, Collembola, Protura, Diplura, Symphyla and Enchytraeidae, as well as smaller forms of spiders, pseudoscorpions, and insect larvae. Macrofauna, organisms >2 mm wide, are the most conspicuous animals within the soil ecosystem (Linden et al.1994) and include Oligochaeta, Gastropoda, and larger Chilopoda, Diplopoda, Araneae, Coleoptera, Isopoda, Opiliones and other insect groups. Although generally less abundant numerically than soil mesofauna, macrofauna can represent a significant proportion of the animal biomass in the soil (see Battigelli et al. 1994).

Oribatida (or Cryptostigmata) are one of the most numerically dominant taxa of soil arthropods (Wallwork 1983, Norton 1990), with densities reaching several hundred thousand individuals per square meter in the organic horizon (Petersen and Luxton 1982, Battigelli et al. 1994). Approximately 7,000 species have been described worldwide, representing more than 1000 genera belonging to more than 150 families (Balogh and Balogh 1992) and all are closely tied to soil habitats (Norton 1990, Behan-Pelletier 1999).

Oribatid mites are long-lived, with low metabolic rates and slow development times. Although this inhibits their ability to take advantage of rapid changes in food resources, low metabolic rates enable them to survive periods of low food intake (Mitchell 1977). Oribatid species have developed various reproductive strategies. Certain oribatid species living in the litter oviposit

throughout the year while those species in the fermentation or humus zones reproduce seasonally, usually ovipositing in spring or summer (Mitchell 1977). These two factors result in a considerable overlap of generations producing relatively stable population densities in most undisturbed soils. Iteroparity, repeated reproduction by the same female, is common among oribatid mites (Norton 1990). Some oribatid families, such as Eremaeidae, Camisiidae, Oppiidae and Tectocepheidae, also demonstrate thelytoky whereby all reproduction is parthenogenetic and males are absent (Perrot-Minnot and Norton 1997). As a reproductive strategy, thelytoky provides members of these families with great colonization abilities in disturbed habitats since the chances of opposite sexes encountering each other may be remote. This is especially important since most oribatid species are poor dispersers (Siepel 1996). With these attributes, oribatid mites would be useful as biological indicators of disturbance in terrestrial ecosystems (Wallwork 1983, Behan-Pelletier 1999).

Soil fauna play a variety of functional roles in soil processes. Via grazing, they control bacterial and fungal biomass thus liberating immobilized nutrients and stimulating further fungal and bacterial activity, as well as enhancing plant growth (Parkinson 1988, Setälä 1995). Furthermore, soil fauna transport microbial propagules and spores into new substrates (Kethley 1990, Norton 1990) and contribute to the development of soil structure and humus formation through the deposition of fecal pellets (Pawluk 1985, Hendrix et al. 1990). Soil nutrients accumulate in faunal biomass and are released back into the soil ecosystem when organisms die. Soil fauna activity is also used in soil humus

classifications (Green et al. 1993) and precise species identification could characterize different soil types (Rusek 1989).

Silvicultural practices, such as forest harvesting and site preparation, modify a variety of physical and chemical properties in the soil, consequently affecting soil pore space, composition and amount of organic matter, forest floor and mineral soil temperatures and soil moisture. Alteration of these properties, in turn, can adversely affect soil fauna density and diversity (Hill et al. 1975, Cancela da Fonseca 1990, Marshall 1993) as well as alter their living space and food supply (Shaw et al. 1991).

Two features of the soil ecosystem, organic matter and soil porosity, can be related to all alterable soil properties important for soil productivity (Powers et al. 1990). Organic matter supplies nutrients in soil, influences soil structure (Banerjee and Sanyal 1991) and provides living space for more than 80% of soil fauna and flora in the forest soil ecosystem (Wallwork 1970, Price 1975). Thus, changes to the quality and quantity of organic matter input can directly influence biological activity. Soil porosity, determined by soil structure and texture, directly influences soil physical properties such as aeration, water storage, infiltration and flow (Childs et al. 1989) and can be adversely affected by soil compaction. Since most soil fauna do not actively burrow in the soil, but utilize existing channels and openings in the soil to move around, decreased macropore space caused by soil compaction would impede their movement as well as limit oxygen exchange and moisture retention in the soil. Organic matter removal and soil

compaction can reduce the diversity and density of soil fauna and alter the structure of the soil fauna community (Marshall 1993).

Since soil fauna respond to, and are influenced by, soil chemical and physical properties, these organisms may provide an integrative measure of soil conditions and a particular soil's response to disturbance or management practices (Linden et al. 1994). Condition of the soil relates to soil health or soil quality. Both terms have been used interchangeably in the literature. Soil health is considered the preferred term (Doran et al. 1994, Pankhurst et al. 1995) since it "portrays the soil as a living, dynamic entity that functions holistically rather than an inanimate entity whose value depends on its innate characteristics and intended use" (Pankhurst et al. 1995). In effect, soil fauna could be used as biological indicators of soil health (Wallwork 1988, Hogervorst et al. 1993, Pankhurst et al. 1995, van Straalen and Verhoef 1997).

Unfortunately, soil faunas of Canadian soils are poorly understood. Only 53% of the estimated 48,500 species of soil arthropods in North America have been described (Behan-Pelletier and Bissett 1992). Furthermore, <25% of the Canadian oribatid fauna is known at the species level, and basic information on distribution, ecology, life history and functional roles is also limited (Behan-Pelletier 1993). Basic data on density, diversity and distribution of soil fauna is essential to provide a basis for monitoring changes in disturbed ecosystems and using soil fauna as bioindicators (Behan-Pelletier 1999).

Of the 14 biogeoclimatic zones in British Columbia, only four have been studied so far: Coastal Western Hemlock (CWH) (Setälä et al. 1994, Battigelli et

al. 1994, McKey-Fender et al. 1994, Setälä and Marshall 1994, Battigelli and Marshall 1993, Panesar and Marshall 1993, Marshall 1974, Vlug and Borden 1973); Interior Douglas Fir (IDF) (Marshall 1979, Marshall 1980); Coastal Douglas Fir (CDF) (Rusek and Marshall 1995) and Englemann Spruce-Subalpine Fir (ESSF) (Nadel 1995, Battigelli 1993, Lawrence 1986). This is the first study to examine the biodiversity of soil fauna within the Sub-Boreal Spruce (SBS) biogeoclimatic zone of central British Columbia. At present, there is little information on the density and diversity of soil organisms in the SBS zone. Furthermore, both short- and long-term effects of soil compaction and organic matter removal on soil organisms in the SBS are unknown, as are the implications of changes in faunal populations for nutrient cycling and soil fertility.

There were two main objectives for this research. First, I examined the density and structure of the soil meso- and macrofauna communities, in general, and the diversity of oribatid mite species, specifically, in the SBS of central British Columbia. Second, I described the short-term changes in density, structure and diversity of the soil fauna community in response to soil compaction and organic matter removal. This study establishes the basis for monitoring long-term changes of the soil fauna community throughout a full rotation period.

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Chapter 2: Descriptions of the Long-Term Soil Productivity Study sites and a comparison of soil properties before and after treatment application.

This chapter provides a general description of the locations, climates, soils and vegetation of each of the three sites in the Long Term Soil Productivity Study (LTSPS), based on information presented in the Long Term Soil Productivity Establishment Report (Trowbridge et al. 1996). Development history of the LTSPS sites and descriptions of experimental design and treatment application are also presented. Chemical and physical properties of the forest floor and mineral soil are compared among sites before treatment and among treatments (sites pooled) one year after treatment application. Data in this chapter have not yet been published and are presented here in order to facilitate comparison among sites and treatments.

Regional Research Pedologists collected these data at each site following a standardized sampling methodology outlined in the LTSP Establishment Report (Trowbridge et al. 1996). I analyzed pre-treatment data and Marty Kranabetter (Research Pedologist, Prince Rupert Forest Region) analyzed post-treatment data.

2.1 Site descriptions

2.1.1 Site Location

The study was conducted within the Sub-Boreal Spruce (SBS) biogeoclimatic zone in the central interior of British Columbia (Figure 2.1). One site was located, respectively, in each of the Prince George, Prince Rupert and Cariboo Forest Regions as follows:

1) Log Lake: located near km 3.5 on the Chichinka-Log Lake forest road 65 km north of Prince George, B.C. on Highway 97 (54°21', 122°37').
2) Topley: located 12 km north of Topley, B.C. on the east side of the Granisle Highway (54°37', 126°18').
3) Skulow Lake: located approximately 39 km northeast of Williams Lake, B.C. on the Likely Road, adjacent to Skulow Lake (52°20', 121°55').

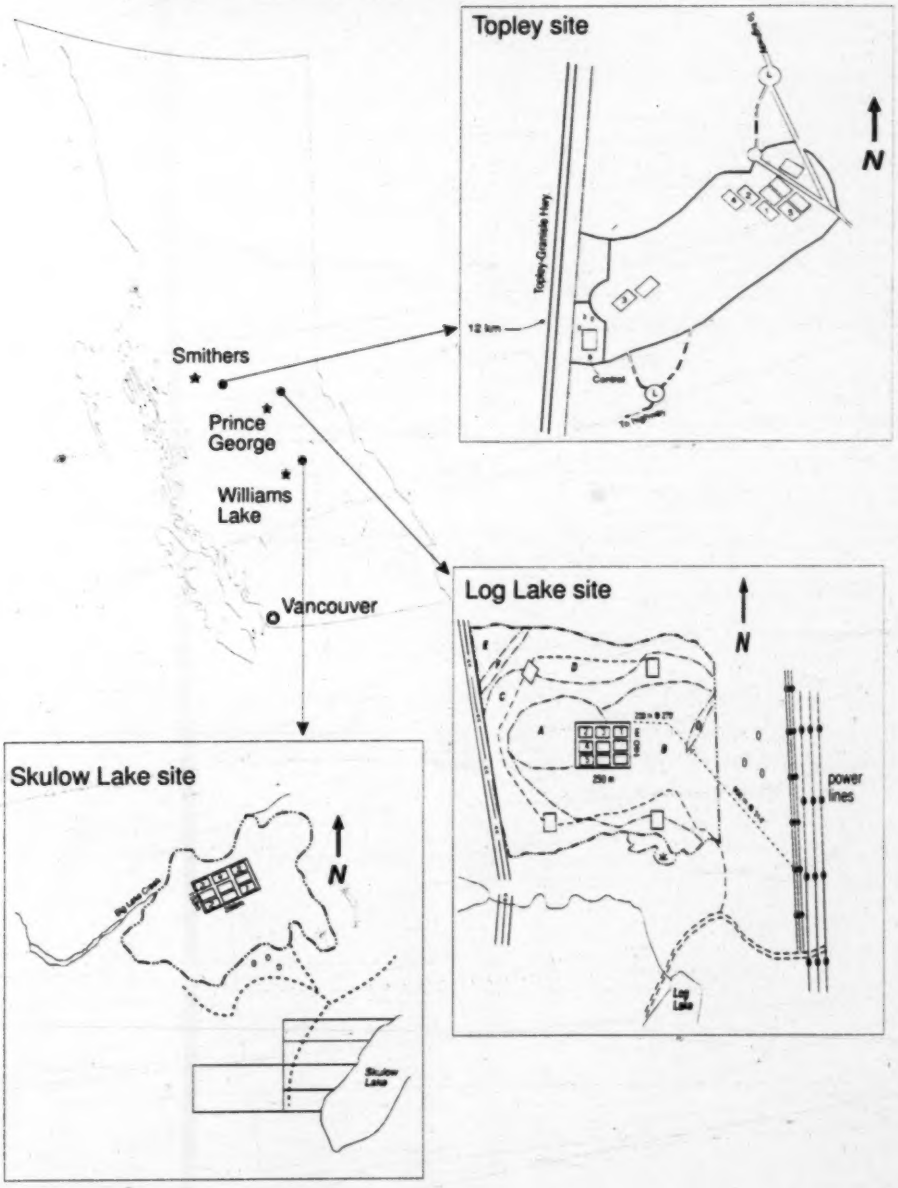
2.1.2 Climate

The SBS has a continental climate with snowy, cold winters and short, warm and moist summers. Mean annual temperature ranges from 1.7 to 5° C, with temperatures below 0° C for 4-5 months of the year and above 10°C for 2-5 months. Mean annual precipitation ranges from 415 to 1650 mm, with snow accounting for approximately 25-50% (Meidinger et al. 1991).

Each site was located in different subzones within the SBS, covering the range of climatic conditions within Sub-Boreal Spruce forests. The SBSwk

Figure 2.1. Site locations and plot layout.

0: control (OM0C0)
1: stem only/no compaction (OM1C0)
2: whole tree forest floor/no compaction (OM3C0)
3: whole tree/medium compaction (OM2C1)
4: stem only/heavy compaction (OM1C2)
5: whole tree-forest floor/heavy compaction (OM3C0)



subzone (Log Lake) has a wet (w) and cool (k) climate with an average temperature of 3.7°C and 614.7 mm of precipitation (see Figure 2.2a). The SBSmc (Topley) subzone has a moist (m) and cold (c) climate with an average annual temperature of 2.8°C and 529.3 mm of precipitation (Figure 2.2b). The SBSdw (Skulow Lake) subzone has a drier (d) and slightly warmer (w) climate than the previous two sites with an average annual temperature of 4.1°C and precipitation of 426.0 mm (see Figure 2.2c). Snow is present on all three sites for at least 5 months of the year when average temperatures are below freezing.

Temperature and precipitation data for all three sites were within normal ranges (see Figures 2.3-5) during the sampling years (data provided by Environment Canada, 1997). At both Log Lake (Figure 2.3) and Topley (Figure 2.4), temperatures were slightly cooler during 1993 than 1992 and 1994. Precipitation was greater at Log Lake during 1992 (607 mm) than either 1993 (503 mm) or 1994 (586 mm) while at Topley, 1994 was a wetter year (583 mm) than either 1992 (456 mm) or 1993 (565 mm). At Skulow Lake (Figure 2.5), 1994 was a warmer year and there was more precipitation during 1995 (582 mm) than 1993 (453 mm) or 1994 (402 mm).

2.1.3 Vegetation

Climax tree species in the SBS are hybrid white spruce (Picea engelmannii x glauca [Moench] Voss) and subalpine fir (Abies lasiocarpa [Hook.] Nutt). Lodgepole pine (Pinus contorta [Engelm]), Douglas-fir (Pseudotsuga

Figure 2.2. Ecological climate diagram for each study site.

Left ordinate is temperature. Values from top to bottom are highest temperature recorded, mean daily maximum temperature of warmest month, mean daily minimum temperaure of coldest month and lowest temperature recorded.

Right ordinate is precipitation. Grey shading indicates relatively humid periods.

Abscissa is months beginning with January. Black bar indicates months with mean daily temperature below 0°C.

Information at the top of each diagram includes station name, (elevation), mean annual temperatue, mean annual precipitation and [number of years of observation].

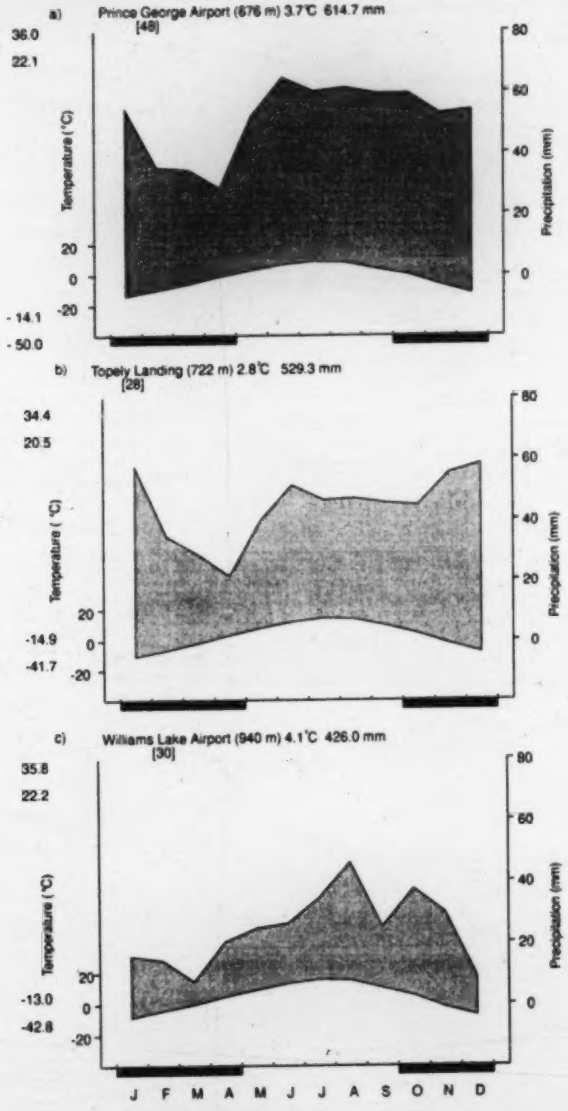


Figure 2.3. Mean daily temperature (°C) [line] and total precipitation (mm) [bar] for Log Lake site using data collected at Prince George Airport from 1992-94.

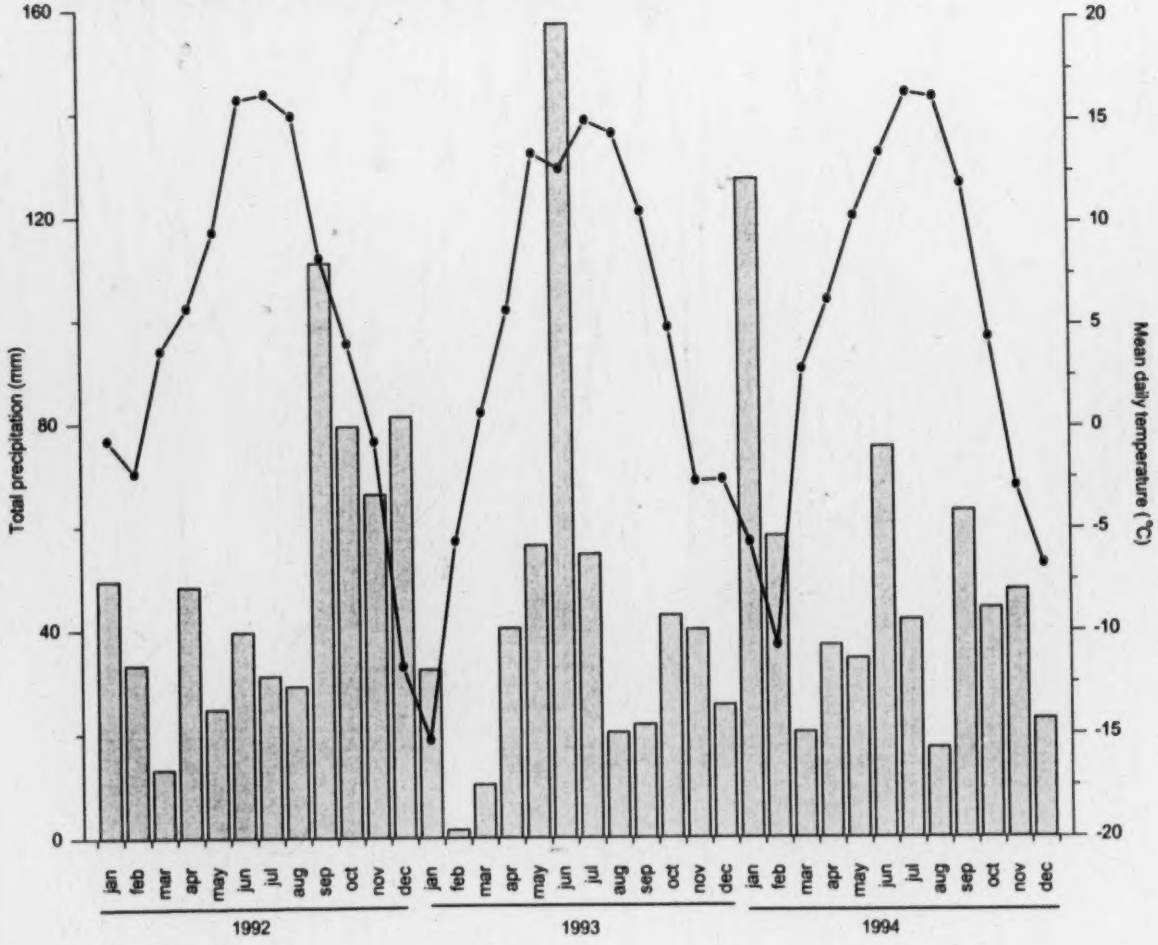


Figure 2.4. Mean daily temperature (°C) [line] and total precipitation (mm) [bar] for Topley site using data collected at Topley Landing from 1992-94.

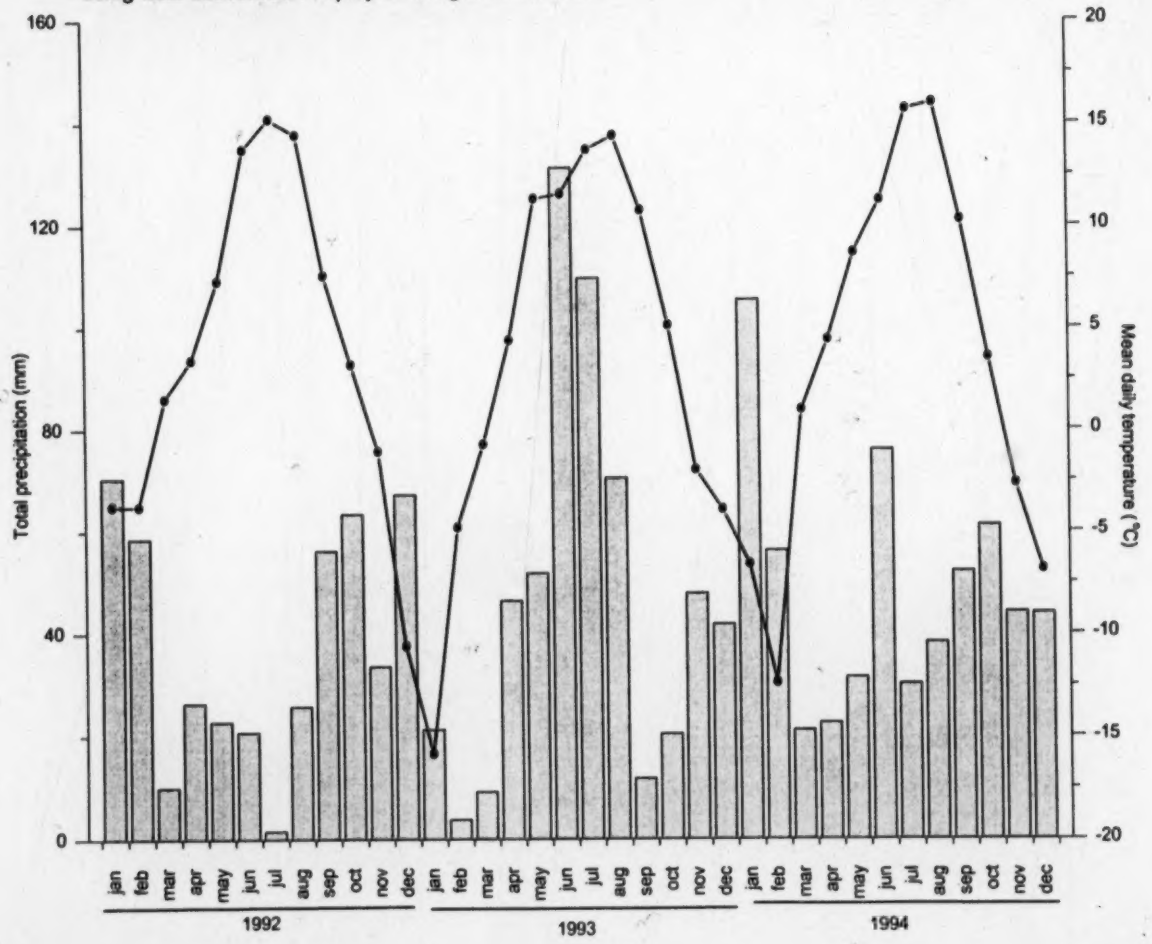
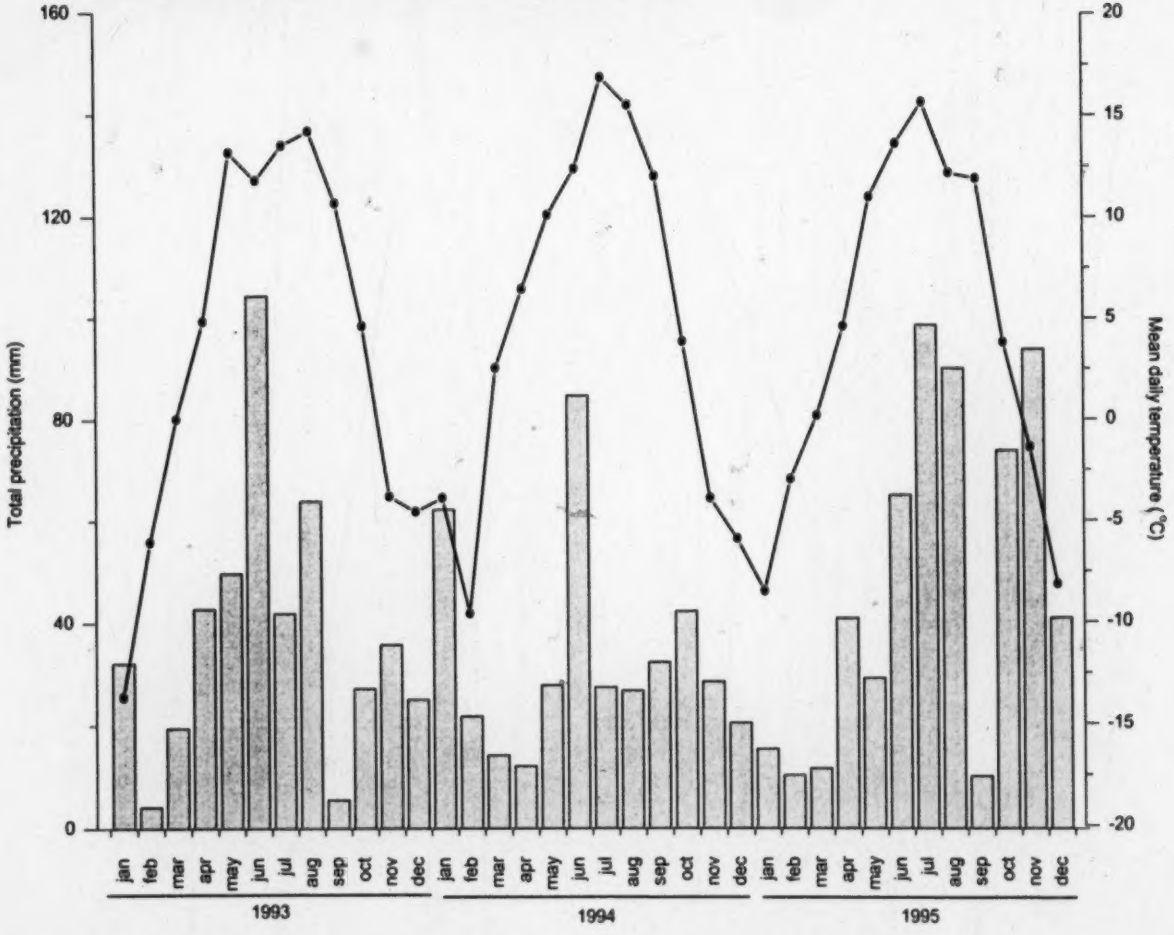


Figure 2.5. Mean daily temperature (°C) [line] and total precipitation (mm) [bar] for Skulow Lake site using data collected at Williams Lake Airport from 1993-95.



menziesii (Mirb.) Franco), trembling aspen (Populus tremuloides Michx.) and paper birch (Betula papyrifera Marsh.) are seral species common in maturing climax forests (Meidinger et al. 1991).

Plots at the Log Lake site (SBSwk) were located in a mature stand approximately 140 years old regenerated after fire. Sub-Alpine fir was the dominant canopy tree (50% cover) followed by Douglas-fir (20%) and hybrid white spruce (11%) with lesser amounts of lodgepole pine and paper birch. Plots at the Topley (SBSmc) site were located in a mature uniform stand 140 years old consisting of Sub-Alpine Fir (40% cover), Lodgepole pine (20% cover) and hybrid-white spruce (17% cover). The stand at the Skulow Lake (SBSdw) site was 112 years old, consisting of co-dominant and dominant lodgepole pine with a suppressed understory of scattered lodgepole pine, hybrid white spruce and trembling aspen. Douglas-fir and P. balsamifera L. are also present in small amounts (Trowbridge et al. 1996)

Understory vegetation (shrub, herb and moss layers) within the sites was relatively uniform, however, the actual proportion of each plant species varied among sites due to differences in climate (see Table 2.1).

Both gross merchantable timber (m^3/ha) and basal area (m^2/ha) for all live trees was substantially lower at Skulow Lake (161 and 19, respectively) than either Log Lake (437 and 47, respectively) and Topley (424 and 50, respectively) based on timber cruise summaries (see Trowbridge et al. 1996).

Table 2.1. Site descriptions (modified from Trowbridge et al. 1996)

Study sites Forest Region	Log Lake Prince George	Topley Prince Rupert	Skulow Lake Cariboo
Biogeoclimatic Zone/subzone	SBSwk	SBSmc	SBSdw
Latitude/Longitude	54° 21'N / 122° 37'W	54° 37'N / 120° 28'W	52° 20'N / 121° 55'W
Elevation (m)	780-790	1100	1050
Slope	0-3%	2-12%	level
Aspect	South	West	not applicable
Landform	Morainal Blanket	Morainal Blanket	Morainal Blanket
Soil classification	OrthicHumo-Ferric Podzol, Gleyed Eluviated Dystric Brunisol, and Orthic Gleysol	Orthic Gray Luvisol, Gleyed Gray Luvisol	Orthic Gray Luvisol
Humus form classification	Hemimor	Hemimor	moder-type
Soil texture	Silt loam over loam	loam to clay loam	loam
Coarse Fragment content (%)	37-41	21-40	30-39
Approximate stand age (years)	140	140	112
Dominant pre-harvest tree species	Abies lasiocarpa, Psuedotsuga mensiesii, Picea glauca x engelmanii	Pinus contorta, A. lasiocarpa, P. glauca x engelmanii	P. contorta, P. glauca x engelmanii, Populus tremuloides
Dominant pre-harvest shrub species	Vaccinium membranaceum Dougl., Rubus parviflorus Nutt., Rosa acicularis Lindl.	V. membranaceum, Lonicera involucrata (Rich.) Banks , R. parviflorus	Sheperdia canadensis Nutt., R. acicularis, Salix spp.
Dominant pre-harvest herb species	Cornus canadensis L., Aralia nudicaulis L., Clintonia uniflora (Schult.) Kunth, Disporum hookeri (torr.) Nichol	C. canadensis, R. pedatus J.E. Smith, Linnaea borealis L., Lycopodium annotinum L.	Hieracium spp., Calamagrostis rubescens Buckl., C. canadensis, Oryzopsis asperifolia Michx., L. borealis
Dominant pre-harvest moss species	Ptilium crista-castensis (Hedw.) DeNot, Pleurozium scherberi (Brid.) Mitt	P. scherberi, P. crista-castensis	P. crista-castensis, Dicranium polysetum (Sw.) Schwaeger., Peltigera aphthosa (L.) Willd.

2.1.4 Soil and humus descriptions

The SBS is most commonly found on the rolling mountainous and plateau landscapes of the central interior of British Columbia with Luvisolic, Podzolic, or Brunisolic soils (Canadian Soil Survey Committee 1987) developed on extensive and often deep deposits of coarse- to fine-loamy textured glacial till. Each site in the present study has deep, medium-textured soils, derived from morainal blankets, with average soil moisture and nutrients for the subzone (Banner et al. 1993, Delong et al. 1993, Steen and Coupe 1997). A range of soil subgroups was identified at the Log Lake site (see Table 2.1). Only two subgroups were found at the Topley site and one at the Skulow Lake site (Table 2.1). A Hemimor humus form was present at both Log Lake and Topley and a moder-type humus form was identified at Skulow Lake.

2.2 Experimental design of the LTSPS

Each of the three sites is treated as a block in a factorial randomized block design in order to generalize conclusions about the SBS biogeoclimatic zone of the British Columbia central interior (see Hope et al. 1990, Holcomb 1996, Trowbridge et al. 1996). From 1991 to 1993, regional Research Pedologists for each site located and established nine treatment plots (40 x 70 m each) (see Table 2.2 for site histories), representing a factorial combination of three organic matter removal treatments and three soil compaction treatments (Table 2.3). Each site was hand-felled during winter with at least a 50 cm snow

pack and ground

Table 2.2. History of Long-Term Soil Productivity Study installation development.

Installation	Selection Year	Logging Year	Completion of treatment application	Seedlings Planted	Sampling years for soil fauna
Log Lake	1991	1991-92	1993	1994	1992/1994
Topley	1992	1992-93	1993	1994	1992/1994
Skulow Lake	1993	1993-94	1994	1995	1993/1995

Table 2.3. Core treatments of the Long Term Soil Productivity Study.

Organic Matter Retention		Soil Compaction	
OM1	Stem (boles) only removed	C0	No compaction
OM2	Stems and crowns removed (whole-tree harvesting)	C1	Light compaction (2 cm impression into mineral soil)
OM3	Whole-tree and forest floor removed (scalped to mineral soil)	C2	Heavy compaction (4 cm impression)

skidded on trails between plots to minimize soil disturbance. In the summer following harvest, logging slash was removed by hand from the OM2 (whole tree removal) and OM3 (whole tree-forest floor removal) plots. Forest floors (L, F and H layers) in the OM3 plots were carefully removed with an excavator and bucket attachment, with as little mineral soil displacement as possible. Compaction treatments were also carried out in the summer, when soil moisture was near field capacity. Compaction depths of 2 and 4 cm were selected to achieve a 40% (light) (C1) and 80% (heavy) (C2) increase in bulk density, respectively,

from pre-harvest conditions to a hypothetical growth-limiting maximum. Compaction was done with an excavator and tamping plate, rather than logging equipment, to better control the uniformity and intensity of compaction. On stem-only removal plots (OM1), logging slash was piled into rows to allow for the compaction treatment and then re-spread. For further information on treatment application see Trowbridge et al. 1996

2.3 Sampling for soil chemical and physical properties

Selected chemical and physical properties of forest floor and mineral soils were measured before harvesting (pre-treatment) and 1 year after treatments were applied (post treatment). Methodologies for these core measurements were initially agreed upon but some small differences in approach by each researcher were found after the work was completed (see Trowbridge et al. 1996).

Bulk density of mineral soil was determined from excavations of approximately 1 litre, from 0 to 20 cm in depth. Either glass beads or foam were used to determine the volume of the holes. Soil sample mass of both coarse fragments and fine fraction were determined separately by sieving through a 2 mm sieve. Forest floor mass and bulk density were determined from a 15 x 15 or 20 x 20 cm area, depending on site, with live roots removed from the sample. Forest floor depth was measured from the four sides of the bulk density excavation. Ten bulk density samples were randomly located and sampled in

each plot pre- and post-treatment.

Five intact soil cores (5 cm diameter x 2 cm height) were randomly taken at near surface (0-1 cm) and 10 cm depths from each plot for aeration porosity. Aeration porosity was determined on the whole core using pressure plates at 10kJ tension.

Chemistry samples were collected from each plot using a stratified technique with five transects across each plot. Five subsamples were collected from each transect and combined. Mineral soil samples were collected using a stony soil auger from a 0-20 cm depth in the mineral soil. Forest floor samples consisted of approximately 500 ml of forest floor (L, F and H layers) removed from the same point. The number of samples collected at the Skulow Lake site differed from Topley and Log Lake, with three subsamples, collected from 18 systematic locations, combined.

The methods for chemical analysis followed Kalra and Maynard 1991 and Carter 1993. Mineral soil and forest floor samples were air dried, ground, and sieved through a 2 mm sieve before chemical analysis. Total C and N were measured using combustion elemental analysis. Mineralizable N was determined through a two-week anaerobic incubation at 30°C, followed by a KCl extraction and colorimetric analysis for ammonium N. Exchangeable cations and cation exchange capacity (CEC) were determined through the neutral ammonium acetate method.

2.4 Statistical analysis of soil chemical and physical properties

A one-way ANOVA procedure was used to compare pre-treatment chemical and physical properties of the forest floor and mineral soil (using proc GLM; SAS Inc. 1990). Alpha was set at 0.05.

Post-treatment effects on chemical and physical properties of the forest floor and mineral soil of the LTSPS factorial design were tested by ANOVA, with site and site interactions as random factors (using proc mixed; SAS Inc. 1990). Plot means for each property were used as a covariate in the analysis. Significant differences between treatment levels were tested by contrasts, with alpha set at 0.10. Time effects were not tested in this analysis.

2.5 Pre-treatment comparison

Prior to treatment application, various soil chemical and physical properties differed significantly among sites (Table 2.4). In general, Topley had significantly higher values for all chemical properties in both the forest floor and mineral soil. Values for Skulow Lake were consistently lower than Log Lake or Topley except for magnesium and pH in both the forest floor and mineral soil. Significant differences in forest floor and mineral soil physical properties among all three sites were also observed (Table 2.4). Forest floor mass (4.1 kg/m^2), bulk density (82 kg/m^3) and depth (5.2 cm) were all significantly lower at Skulow Lake than at

Table 2.4. Comparison of soil chemical and physical properties among all three sites prior to treatment application. Means followed by the same letter are not significantly different according to Tukey's test (α=0.05).

	Log Lake		Topley		Skulow Lake	
Aeration Porosity (%)						
Surface	25.1		24.1		20.9	
Subsurface	16.6		17.1		17.5	
Forest Floor						
Mass (kg/m^2)	7.8 ±0.53	a	7.6 ±0.53	a	4.1 ±0.56	b
Bulk Density (Kg/m^3)	112 ±0.5	a	114 ±0.5	a	82 ±0.5	b
Depth (cm)	7.1 ±0.37	a	6.6 ±0.37	a	5.2 ±0.39	b
C (Kg/ha)	28931 ±549.6	b	36412 ±549.6	a	16004 ±409.6	c
N (Kg/ha)	882 ±28.0	b	1062 ±28.0	a	514 ±20.8	c
C:N Ratio	33 ±0.7	ab	34 ±0.7	a	31 ±0.5	b
mineralizable N (Kg/ha)	22 ±1.9	b	30 ±1.9	a	14 ±1.4	c
Total S (Kg/ha)	97 ±5.1	b	114 ±5.1	a	42 ±3.8	c
Available P (Kg/ha)	8 ±0.4	a	7 ±0.4	b	5 ±0.3	c
CEC (cmol+/kg)	41 ±1.7	c	110 ±1.7	a	77 ±1.2	b
Ca (Kg/ha)	515 ±27.1	a	483 ±27.1	a	233 ±20.2	b
K (Kg/ha)	68 ±4.3	b	95 ±4.3	a	66 ±3.2	b
Mg (Kg/ha)	37 ±4.3	c	59 ±4.3	b	89 ±3.2	a
pH (H2O)	4.4 ±0.05	b	4.4 ±0.05	b	5.0 ±0.04	a
pH (CaCl2)	4.1 ±0.05	b	4.1 ±0.05	b	4.6 ±0.04	a
Mineral Soil						
Coarse Fragment content (% vol.)	34		30		19	
Total bulk density (g/cm^3) (total weight/total volume)	1.6 ±0.05	a	1.4 ±0.05	b	1.6 ±0.05	a
Fine Fraction Bulk Density (g/cm^3) [<2mm]	1.0 ±0.04	b	1.0 ±0.04	b	1.3 ±0.04	a
Bulk Density for nutrient calculation (g/cm^3)	0.66		0.77		1.05	
C (Kg/ha)	21009 ±2901.6	b	48575 ±2901.6	a	23455 ±1529.3	b
N (Kg/ha)	1159 ±161.8	c	2310 ±161.8	a	1742 ±85.3	b
C:N Ratio	19 ±0.6	b	21 ±0.6	a	14 ±0.3	b
mineralizable N (Kg/ha)	13 ±5.3	c	48 ±5.3	a	33 ±2.8	b
Total S (Kg/ha)	72 ±9.7	c	205 ±9.7	a	91 ±5.1	b
Available P (Kg/ha)	70 ±5.4	a	13 ±5.4	c	30 ±2.8	b
CEC (cmol(+)/kg)	23 ±1.4	a	24 ±1.4	a	12 ±0.8	b
Ca (Kg/ha)	609 ±247.8	c	2797 ±247.8	a	1828 ±130.6	b
K (Kg/ha)	82 ±8.6	b	143 ±8.6	a	124 ±4.5	a
Mg (Kg/ha)	67 ±56.3	a	571 ±56.3	b	1110 ±29.7	a
pH (H2O)	4.7 ±0.07	c	5.1 ±0.1	b	5.8 ±0.04	a
pH (CaCl2)	4.3 ±0.07	c	4.6 ±0.07	b	4.8 ±0.04	a

Topley (7.6 kg/m^2, 114 kg/m^3, 6.6 cm) or Log Lake (7.8 kg/m^2, 112 kg/m^3, 7.1 cm).

2.6 Post-treatment comparisons

Overall, organic matter removal and soil compaction had a limited effect on mineral soil and forest floor chemistry after one year (Table 2.5). In the mineral soil, total carbon and exchangeable K were significantly influenced by organic matter removal. A significant organic matter removal by soil compaction interaction was observed for both mineralizable N and pH in the mineral soil. Forest floor pH was significantly influenced by soil compaction.

Only exchangeable K in the mineral soil showed clear treatment effects of both organic matter removal and soil compaction in the comparison of nutrient mass for post treatment sampling (Table 2.6). Significant organic matter removal and soil compaction for available P in the mineral soil and mineralizable N in both the mineral soil and forest floor were also observed in the comparisons of nutrient mass (Table 2.6).

Bulk density increased significantly after compaction treatments (Table 2.7). Compaction or organic matter removal did not affect aeration porosity or forest floor mass (Table 2.7).

Slash loading on stem-only removal plots (OM1) was approximately 30 tonnes per hectare in total, with logs greater than 7 cm in diameter making up the majority of slash. Slash loads of OM1 plots did not differ significantly across compaction treatments (Table 2.8).

Table 2.5. Impact of organic matter removal (OM) and compaction (Comp) (year 1) on mineral soil and forest floor chemistry [mean values (±SE)]. P values are presented and bold text indicates a significant difference.

Mineral soil	C (%)	N (%)	S (%)	Avail P (ppm)	C/N	Min N (ppm)	CEC	Ex Ca	Ex Mg	Ex K	pH (H_2O)
							(cmol/100 g)				
Pre-treatment	1.88	0.11	0.007	26.2	17.2	19.5	18.0	4.96	2.40	0.19	5.22
	(0.41)	(0.016)	(0.002)	(16.4)	(1.9)	(6.0)	(2.7)	(1.65)	(1.27)	(0.03)	(0.30)
Post-treatment	1.49	0.08	0.006	20.0	19.0	22.4	13.4	4.92	2.90	0.17	5.53
	(0.41)	(0.016)	(0.002)	(16.4)	(1.9)	(6.0)	(2.7)	(1.65)	(1.27)	(0.03)	(0.30)
OM	**0.0954**	0.2179	0.9713	0.7377	0.3145	0.1110	0.3080	0.6213	0.5305	**0.0321**	0.1529
Comp	0.8828	0.4818	0.6275	0.4738	0.5002	0.2670	0.9204	0.6409	0.8156	0.4846	0.2332
OmxComp	0.3015	0.1414	0.1094	0.1945	0.5422	**0.0955**	0.2967	0.5801	0.4235	0.2303	**0.0403**

Forest floor	C (%)	N (%)	S (%)	Avail P (ppm)	C/N	Min N (ppm)	CEC	Ex Ca	Ex Mg	Ex K	pH (H_2O)
							(cmol/100 g)				
Pre-treatment	40.7	1.24	0.124	93.2	32.7	339	77.9	30.7	9.2	3.00	4.64
	(2.02)	(0.04)	(0.012)	(23.1)	(0.74)	(16)	(13.3)	(2.2)	(4.2)	(0.72)	(0.16)
Post-treatment	44.5	1.23	0.115	167.1	37.0	537	76.3	36.4	10.7	3.11	4.99
	(2.05)	(0.04)	(0.012)	(75.8)	(0.87)	(20)	(13.3)	(2.3)	(4.2)	(0.73)	(0.16)
OM*	0.1936	0.2978	0.8831	0.5877	0.1032	0.5272	0.6085	0.7249	0.6137	0.8161	0.1740
Comp	0.5875	0.3259	0.1550	0.4716	0.1638	0.7091	0.7706	0.8966	0.8607	0.2689	**0.0426**
OmxComp	0.5488	0.8095	0.8831	0.2986	0.3076	0.7730	0.4109	0.3241	0.3897	0.3908	0.1718

*OM3 not included because forest floors were removed

Table 2.6. Effect of organic matter removal (OM) and compaction (Comp.) on soil nutrient mass (mean+ SE) 1 year after treatment. P values are presented and bold text indicates significant result.

	C	N	S	Available P	Mineralizable N	Exchangeable Ca	Exchangeable Mg	Exchangeable K
					(kg/ha)			
Mineral soil								
Pre-treatment	29921 (7751)	1664 (350)	118 (36)	37 (24)	30 (13)	1666 (692)	537 (300)	105 (28)
Post-treatment	27596 (7751)	1523 (350)	116 (36)	38 (24)	45 (13)	1895 (692)	637 (300)	122 (28)
OM	0.2001	0.3641	0.8164	0.7598	0.1911	0.7134	0.4178	**0.0912**
Comp.	0.1240	0.2248	0.3412	0.9921	0.4009	0.1714	0.7211	**0.0698**
OM*Comp.	0.2690	0.6819	0.1759	**0.0833**	**0.0471**	0.7962	0.5764	0.5765

	C	N	S	Available P	Mineralizable N	Exchangeable Ca	Exchangeable Mg	Exchangeable K
					(kg/ha)			
Forest floor								
Pre-treatment	27063 (6067)	815 (168)	84 (21)	6.4 (1.0)	21.9 (5.4)	414 (109)	61 (14)	75 (4)
Post-treatment	28170 (6209)	779 (172)	74 (22)		34.2 (5.8)	490 (112)	69 (14)	52 (6)
OM*	0.8024	0.5676	0.5688	0.4875	0.6734	0.5071	0.7278	0.1340
Comp.	0.5168	0.9349	0.9255	0.8168	0.1724	0.9134	0.8814	0.1582
OM*Comp.	0.2407	0.1485	0.1516	0.3370	**0.0049**	0.2947	0.4864	0.4363

*OM3 not included because forest floors were removed

Table 2.7. Effect of organic matter removal (OM) and compaction (Comp.) on mean soil physical properties (+SE) 1 year after treatment application. P values are presented and bold text indicates a significant difference.

	Bulk density (g/cm^3)	Aeration porosity (% of total vol.)	Forest Floor mass (kg/m^2)
Pre-treatment	1.07 (0.04)	20.5 (0.8)	6.48 (1.3)
Post-treatment	1.39 (0.04)	13.8 (0.8)	6.24 (1.3)
OM	0.7589	0.2905	0.8481*
Comp	**0.0591**	0.1117	0.6959
OM*Comp	0.5688	0.5178	0.1936

* OM3 not included because forest floors were removed.

Table 2.8. Slash loading by diameter size class [mean(+SE)] (tonnes/ha)

Size class diameter (cm)	≤ 0.5	0.6 to 1.0	1.1 to 3	3.1 to 5	5.1 to 7	> 7	Total slash
Post-treatment	0.7 (0.08)	1.2 (0.1)	2.9 (0.2)	2.1 (0.2)	2.3 (0.2)	22.6 (2.4)	31.7 (3.2)
Comp	0.7122	0.5924	0.6975	0.8656	0.9442	0.4707	0.4871

Soil temperatures were measured at 30 cm above ground and at 2, 10 and 30 cm below ground for one year after treatment application. Daily mean average temperatures fluctuated more on those plots where the forest floor has been removed compared to stem-only harvested plots (Figures 2.6-2.8). On the plots with whole tree and forest floor removal, soil temperatures were colder in winter and warmer in summer. Furthermore, soils in plots with whole tree and forest floor removal had significantly more freeze/thaw events (soil temperatures <-1°C) (M. Kranabetter unpublished results). Further examination of soil temperature could reveal sufficiently high enough temperatures at certain times of the day which could be lethal to soil organisms.

Figure 2.6. Daily mean air (at 30 cm above ground) and soil (at 2 cm, 10 cm, and 30 cm below ground) temperatures (°C) taken for one year (September 20, 1996 – September 20, 1997) after treatment application at Log Lake.

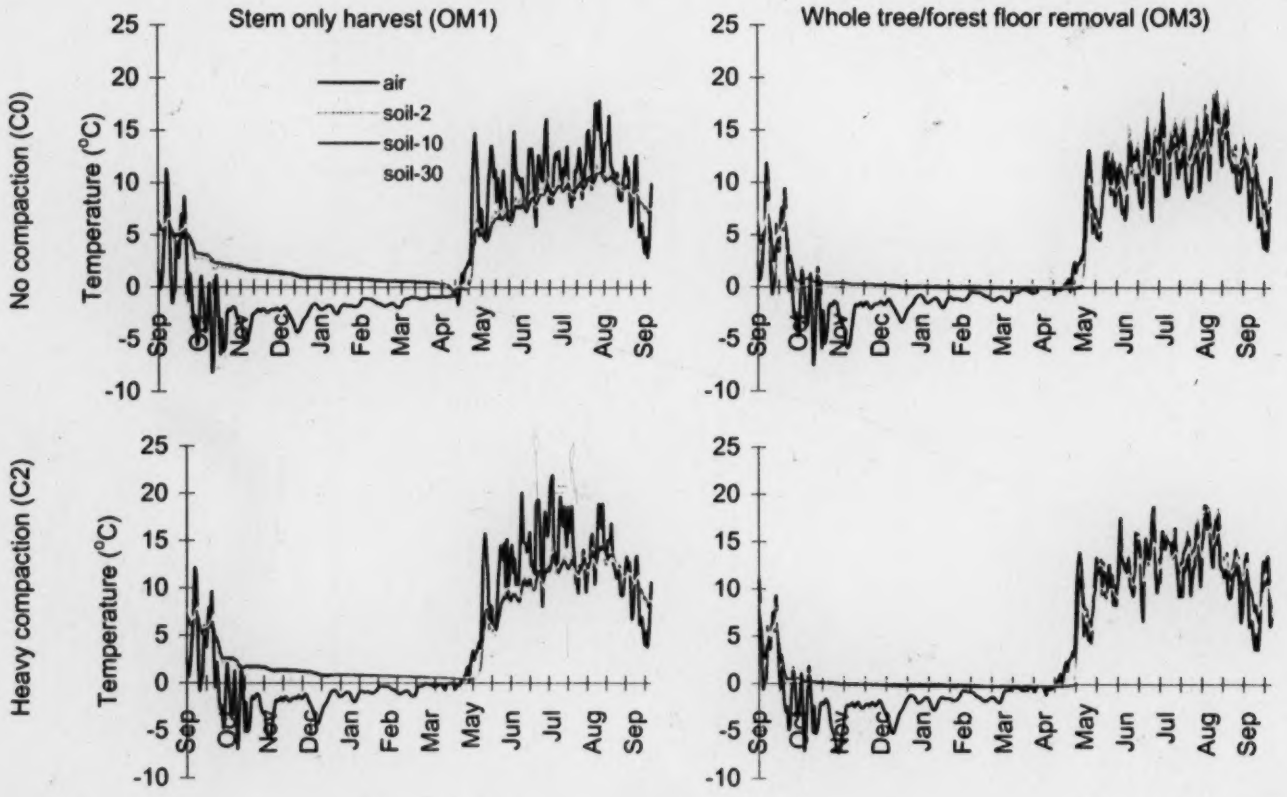


Figure 2.7. Daily mean air (at 30 cm above ground) and soil (at 2 cm, 10 cm, and 30 cm below ground) temperatures (°C) taken for one year (September 20, 1996 – September 20, 1997) after treatment application at Topley.

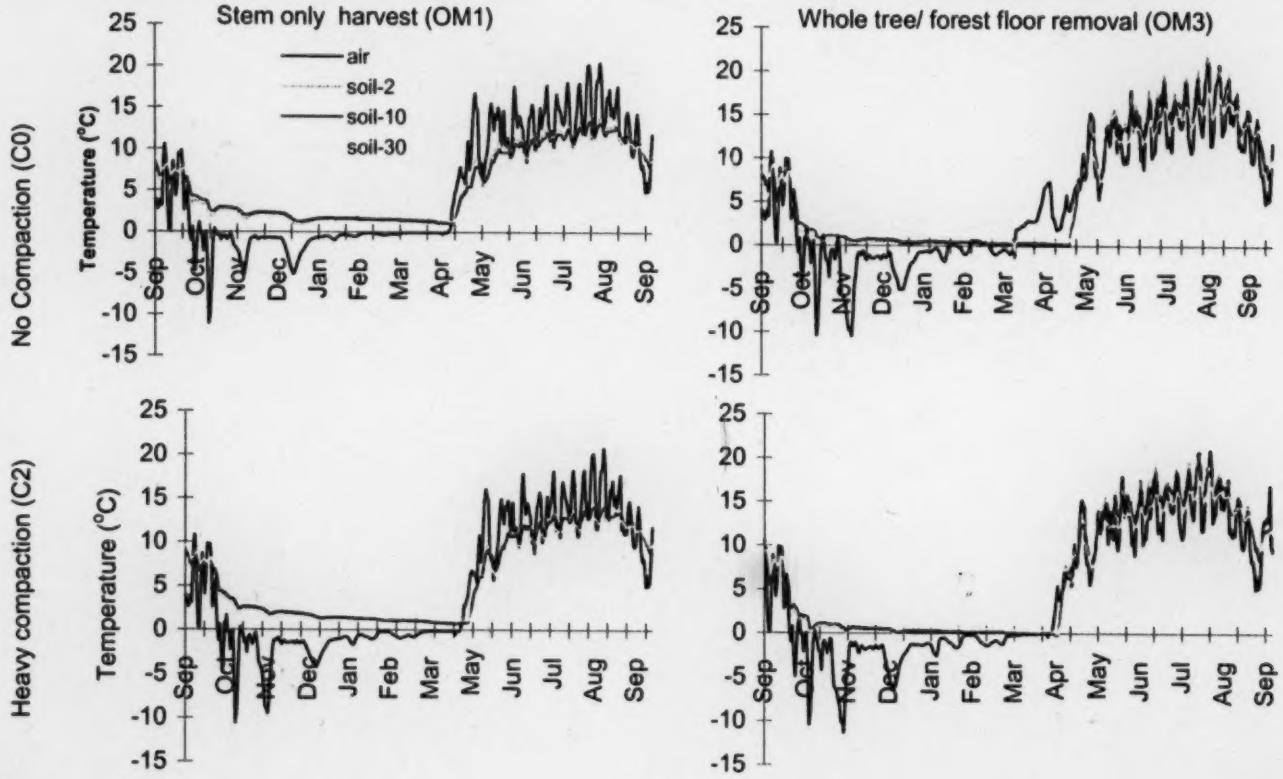
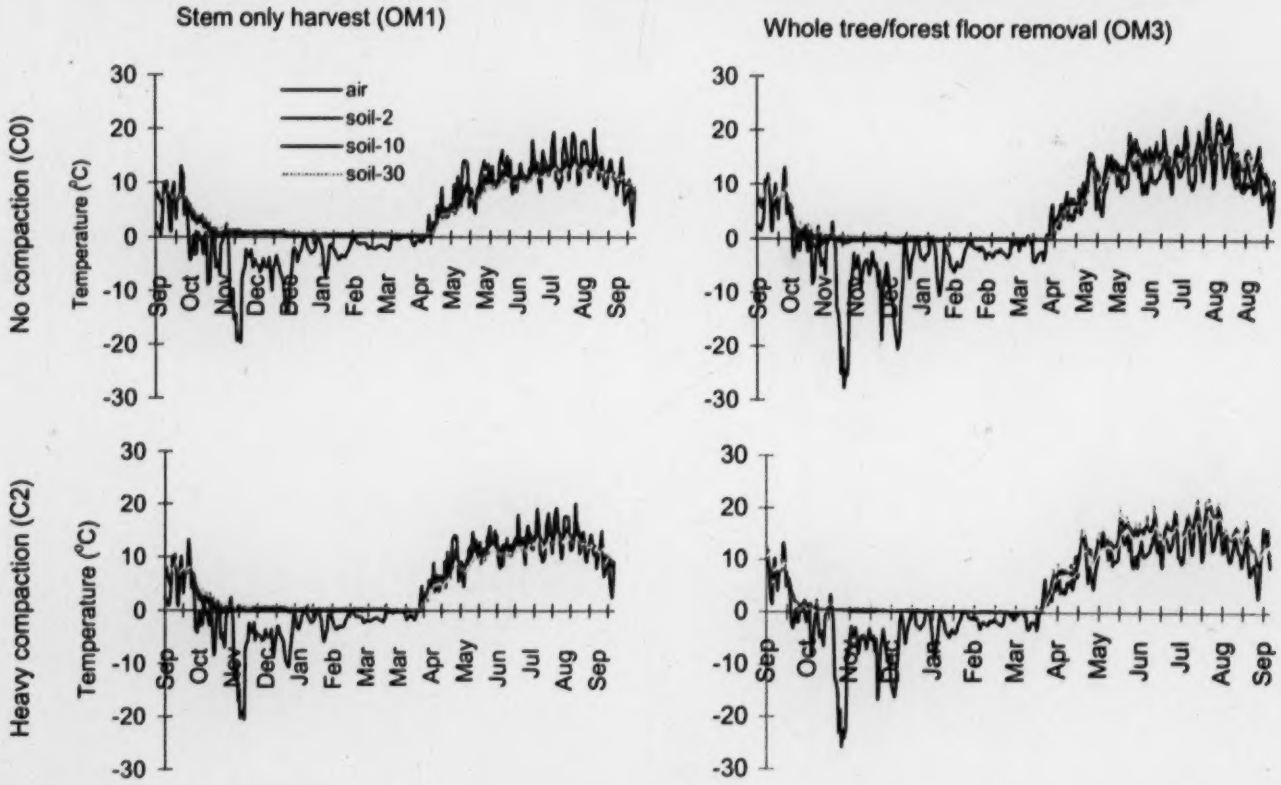


Figure 2.8. Daily mean air (at 30 cm above ground) and soil (at 2 cm, 10 cm, and 30 cm below ground) temperatures (°C) taken for one year (September 20, 1996 – September 20, 1997) after treatment application at Skulow Lake.



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Chapter 3: Short-term impact of organic matter removal and soil compaction on soil macrofauna.

3.1 Introduction

Soil macrofauna, organisms > 2 mm in body width (Swift et al. 1979), are the most conspicuous animals within the soil ecosystem (Linden et al.1994). Included in this group are ants, termites, isopods, centipedes, millipedes, earthworms, snails and slugs. Although generally less numerous than soil mesofauna, macrofauna can represent a significant proportion of the animal biomass in the soil (see Battigelli et al. 1994) and play an important role in soil ecosystem function. For example, millipedes and earthworms break up organic matter, increasing its surface area and thereby enhancing microbial activity. Initial fragmentation of organic matter by soil macrofauna is critical for the continued success of decomposition and nutrient cycling (Fellin 1979). Soil macrofauna also mix and redistribute mineral and organic material as well as microorganisms within the soil profile (Wallwork 1970). Predatory activity of spiders, centipedes and pseudoscorpions can alter the structure of the microarthropod community (i.e. mites and springtails), resulting in local extinction of certain species and changes to microbial biomass and activity in the soil (Wallwork 1970, Giller 1996). Macrofauna, as well as all other soil fauna, also produce fecal material, which affects soil structure and promotes humification in the soil (Hendrix et al. 1990).

Although soil organisms have a critical role in soil development (Pawluk 1985) and the maintenance of soil fertility (Seastedt 1984), they have been largely ignored in forest soil ecosystems of North America. Knowledge of the abundance, diversity and ecological roles of soil animals in most North American soils are poorly understood due to a lack of intensive studies (Marshall 1993). Only 53% of an estimated 48,500 species of soil arthropods in North America have been described (Behan-Pelletier and Bissett 1992).

In 1991, the British Columbia Ministry of Forests established the Long Term Soil Productivity Study (LTSPS) (see Hope et al. 1991, Powers et al. 1990) in the Sub-Boreal Spruce (SBS) biogeoclimatic zone of central British Columbia. In conjunction with a research program in the United States (see Powers 1989), this study examines the general impact of various levels of organic matter removal and soil compaction on long-term soil productivity. Physical and chemical soil properties as well as plant response will be monitored over a full rotation period (80-120 years) at these SBS sites. Organic matter removal and soil compaction can also adversely affect the diversity, density and structure of the soil fauna community (Marshall 1993).

Establishment of the LTSPS provides an opportunity to examine soil biota in conjunction with physical and chemical properties of soil. At present, there is little information on the density and diversity of soil organisms in the SBS. Furthermore, both short- and long-term effects of these treatments on soil organisms are unknown, as are the implications of changes in faunal populations for nutrient cycling and soil fertility within the SBS.

There are two main objectives for this chapter: first, to examine the density and relative abundance of soil macrofauna at the order level among three sites located within the SBS biogeoclimatic zone of central British Columbia; and second, to determine the short-term (I year after treatment) impact of organic matter removal and soil compaction on this faunal community. This study will establish baseline data for monitoring changes to the soil macrofauna community from these disturbances over a full rotation period in this forest soil ecosystem.

3.2 Materials and Methods

3.2.1 Study site

This study was conducted within the Sub-Boreal Spruce (SBS) biogeoclimatic zone in the central interior of British Columbia (Figure 2.1). Refer to Chapter 2 for further information on site descriptions, plot layout and treatment application at the three replicate installations of the Long Term Soil Productivity Study.

3.2.2 Sampling, extraction and sorting of soil macrofauna

Due to financial and time constraints, samples for macrofauna were collected from only four plots at each installation: the control (OM0-C0); stem only - no compaction (OM1-C0); whole tree - light compaction (OM2-C1); and

stem only - heavy compaction (OM1-C2). These plots matched those plots sampled for mesofauna. Samples included only the organic horizon as most of the macrofauna were expected to be found here.

All four plots at each site were sampled at the same time during the spring, summer and fall one year after treatment application (1994 at Topley and Log Lake; and 1995 at Skulow Lake). Seasons were defined as: bud burst on trembling aspen (spring); soil temperature of 10 °C at 10 cm (summer) and leaf colour change in trembling aspen (fall). These indicators were chosen to standardize sampling times among sites with different phenologies. In addition, they relate to biological activity in the soil and span the range of seasonal variation in distribution and life stages for soil fauna at these sites.

Control plots were subdivided into 0.5 X 0.5 m subplots. Subplots in the treatment plots were 2.5 x 2.5 m, defined by using seedlings already planted on the plots as corners. For each sampling date, three subplots were selected at random in each plot at each site. One 0.3 X 0.3 m sample of forest floor (L, F, and H layers) was removed from the center of each subplot (large rocks and downed logs were avoided when collecting the samples) and placed in a labeled plastic bag in a cooler until processed. Each subplot was sampled only once during the study to limit the impact of soil removal on the sites.

Within 48 hours of collection, samples were placed in Berlese Funnels (see Norton and Kethley 1988) for 1 week. This method collected both meso- and macrofauna. Macrofauna were identified, counted and sorted from this material under a dissecting microscope. Lumbricidae were identified to species using

Reynolds (1977) and the remaining Arachnida, Crustacea and Insecta identified to Order except for Formicidae in Hymenoptera. Mollusca, Myriapoda and the remaining Hexapoda were identified to Class. This level of classification provided a conservative estimate of changes in structure and density of soil macrofauna (Haskell 2000). Taxa can be selected for further intensive study at the species level for the duration of the study provided interest and financial support are available. All mesofauna samples are stored with the B.C. Ministry of Forests Research Branch Laboratory, P.O. Box 9536 Victoria, B.C. V8W 9C4. Arrangement of taxa for all arthropods to class and order follows Scudder et al. (1979).

3.2.3 Data analyses

Density (number of individuals per sample) and percent relative abundance ([number of individuals per taxon/total individuals collected in the sample] x 100) were used in analyses. Density is useful for estimating population size and determining changes in absolute abundance while relative abundance is useful to compare the structure of soil fauna assemblage and the structural similarity among sites, seasons or treatments (Wallwork 1976).

Only taxa representing $\geq$1% of all collected material were considered for further analysis since less numerous taxa did not support meaningful analysis. Data were transformed to meet assumptions of normality before analyses. Density data were log transformed [$\log_{10}$ (X+1) where X = actual count of

individuals for a taxon] and relative abundance data were arcsine transformed (arcsin$\sqrt{p}$ where p = relative abundance of the taxon).

A 2-way ANOVA [sites, seasons (3X3)] was used to compare density and relative abundance of macrofauna among sites and seasons using data collected from uncut forest control plots only. A 3-way ANOVA [sites, treatment, seasons (3 x 4 x 3)] was used to examine the short-term impact of the treatments on density and structure of the macrofauna community. In both analyses, a non-parametric test of ranked scores was used for those taxa that did not have normally distributed data. Statistical significance was judged using Type III sums of squares for all procedures. Test statistics and probabilities are presented for significant differences.

That sampling at Topley and Log Lake occurred one year prior to sampling at Skulow Lake might confound comparisons among the uncut forest control plots of each site. Therefore, year effect is not considered in the analysis of treatment impact, treatment severity is assumed to override year-to-year changes. However, a significant site by treatment interaction was expected since sites were located in different subzones and different operators applied treatments. Therefore, in order to examine the impact of treatments on density, the mean square value of the site-by-treatment interaction was used as the denominator for the F-test. To determine if there was a significant effect due to season or season by treatment interaction, the mean square value of the site-by-treatment-by-season interaction was used as the denominator for the F-test.

If significant differences were found then Tukey's Studentized range test was used to compare means among sites. A non-parametric Tukey-type multiple comparison test was used if differences were found using the non-parametric test of ranked scores (Zar 1984). All statistical tests used in this study were conducted using the SAS General Linear Models (GLM) procedure (SAS 1990) with $\alpha = 0.05$. Density (number of individuals/m^2) and relative abundance (% of total fauna collected) values are reported as mean ± standard error unless stated otherwise.

3.3 Results

3.3.1 Comparison of soil macrofauna among subzones

There was a significant site by season interaction for mean density of total macrofauna ($F_{4,26}$=4.30, p=0.013). Densities of total macrofauna were highest during fall and lowest during summer at both Topley and Skulow Lake (Figure 3.1). However, at Log Lake, densities were highest during summer and lowest during spring. Four other macrofauna taxa also had significant site by season interactions (Figure 3.2). Densities of both Hemiptera ($F_{4,26}$=3.61, p=0.025) and Diptera larvae ($F_{4,26}$=4.22, p=0.014) followed the same pattern as total macrofauna (Figure 3.2a and b, respectively). At Topley and Log Lake, densities of Coleoptera larvae ($F_{4,26}$=3.67, p=0.023) were highest in summer than spring or

Figure 3.1. Significant site by season interaction for density of total macrofauna.

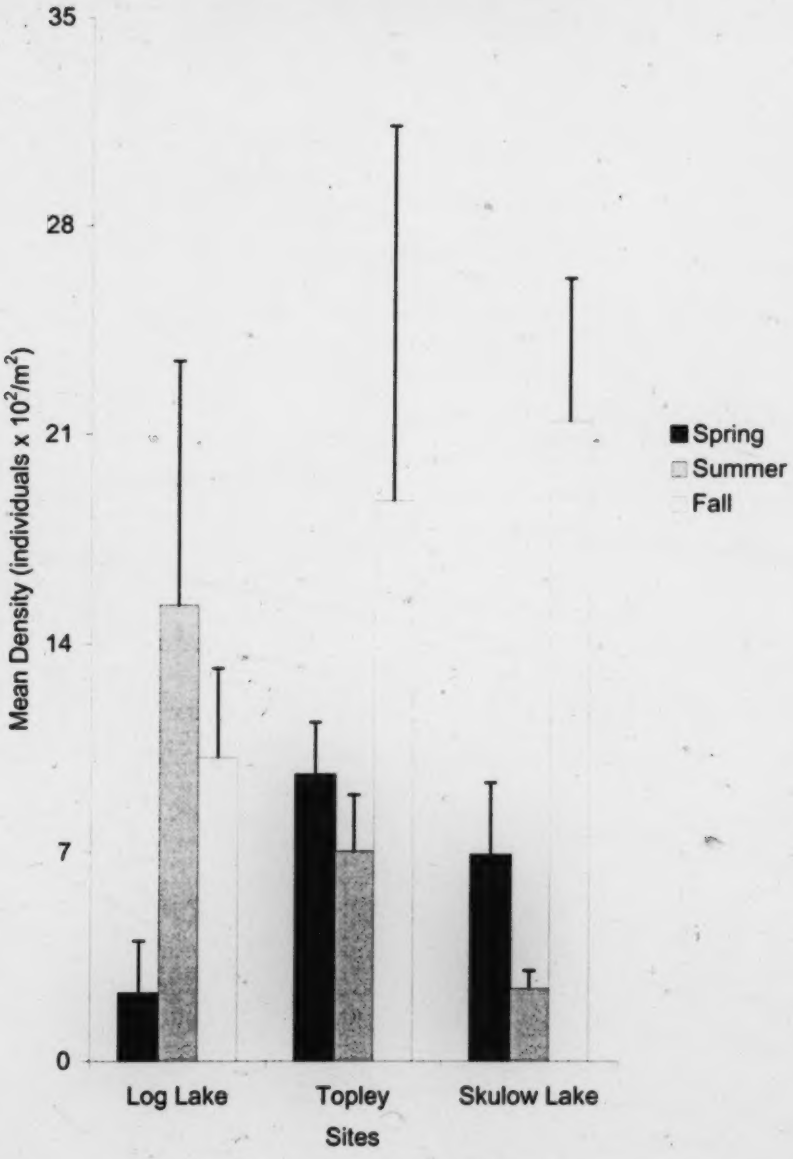
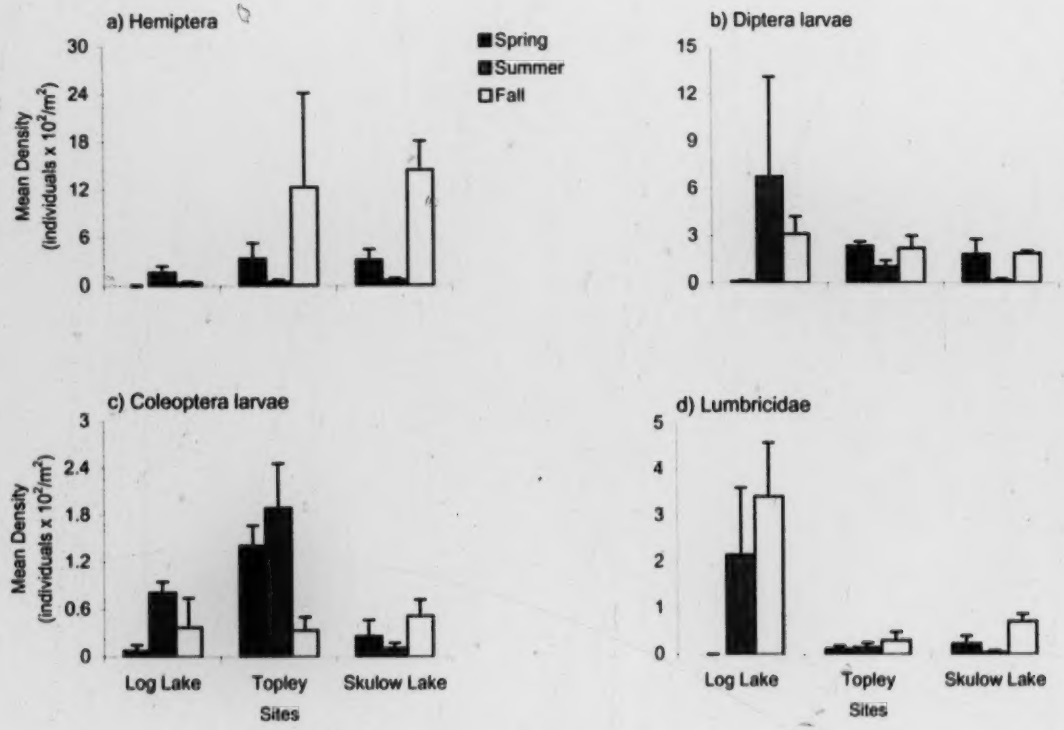


Figure 3.2. Significant site by season interaction for densities of (a) Hemiptera, (b) Diptera larvae, (c) Coleoptera larvae and (d) Lumbricidae.



fall while at Skulow Lake densities were higher during spring and fall than summer (Figure 3.2c). Densities of Lumbricidae ($F_{4,26}$=4.86, p=0.008) increased from spring to fall on all sites and were higher at Log Lake than either Topley or Skulow Lake (Figure 3.2d). Two species of Lumbricidae were collected: Dendrobaena octaedra (Savigny, 1826) was collected at all three sites; and Lumbricus rubellus Hoffmeister, 1843 was collected only at Skulow Lake.

Mean density of six macrofaunal taxa differed significantly among sites (Table 3.1). Densities of Araneae differed significantly among all three sites with densities being greatest at Topley followed by Skulow Lake then Log Lake ($F_{2,26}$=19.86, p<0.0005). Densities of pseudoscorpions ($F_{2,26}$=4.27, p=0.03) and Chilopoda ($F_{2,26}$=13.70, p=0.0002) were higher at Log Lake than Skulow Lake or Topley.

Densities of both Coleoptera adults ($F_{2,26}$=24.05, p<0.00005) and Diplopoda ($F_{2,26}$=4.97, p=0.019) were higher at Log Lake and Topley than at Skulow Lake. Densities of Hymenoptera (excluding Formicidae) differed significantly among all three sites ($F_{2,26}$=10.15, p=0.001), being highest at Skulow Lake followed by Topley then Log Lake (Table 3.1).

Relative abundance of eight macrofauna taxa differed significantly among sites (Figure 3.3a). Relative abundance of spiders was significantly greater at both Topley and Skulow Lake than Log Lake ($F_{2,26}$=14.13, p=0.0002). Relative abundances of both Pseudoscorpionida and Chilopoda were higher at Log Lake than either Topley or Skulow Lake ($F_{2,26}$=6.37, p=0.008 and $F_{2,26}$=20.63, p=0.00002, respectively). Proportions of Hemiptera and Hymenoptera were

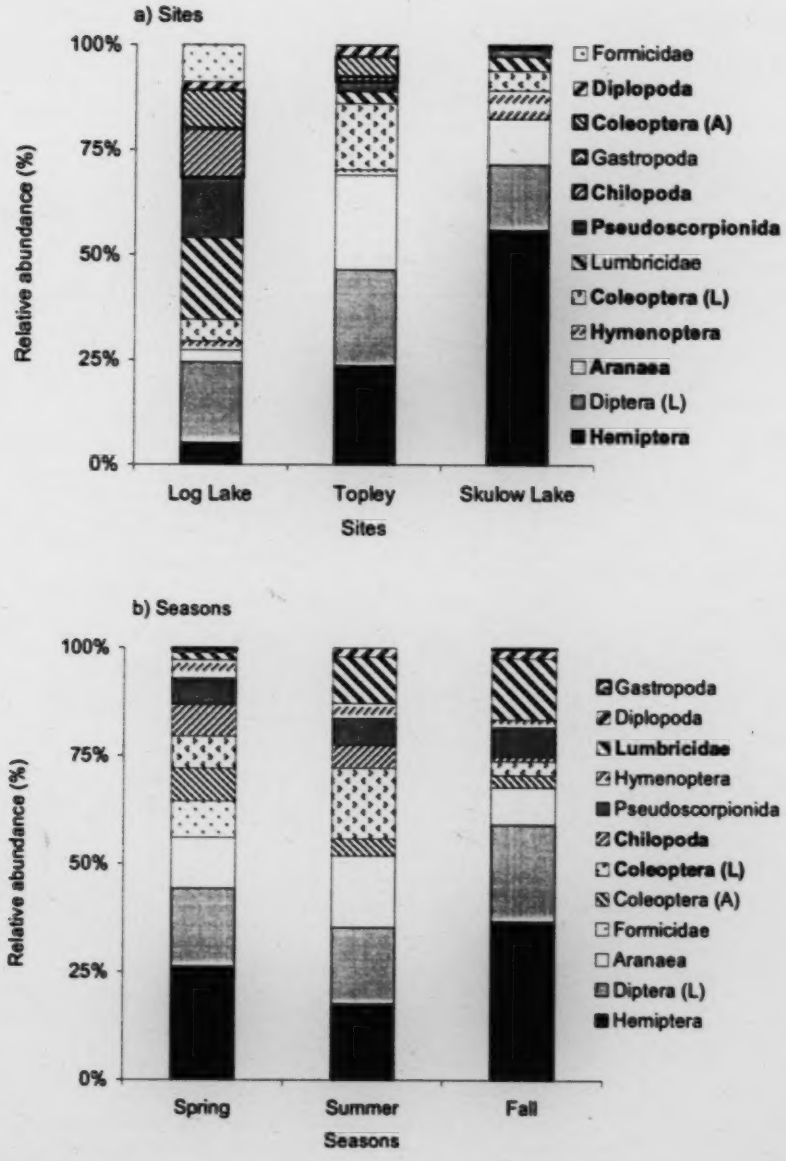
Table 3.1. Comparison of mean density (individuals/m^2) (± SE) of macrofauna among (a) sites and (b) seasons. Means for a taxon followed by blank or same letter are not significantly different (Tukey's test or non-parametric comparison of means, α=0.05).

	a) Site			b) Season		
	Log Lake	Topley	Skulow Lake	Spring	Summer	Fall
Aranaea	10 ± 4.3 [c]	181 ± 36.8 [a]	96 ± 41.3 [b]	75 ± 23.8	94 ± 46.5	119 ± 45.5
Pseudoscorpionida	81 ± 35.2 [a]	20 ± 6.1 [b]	21 ± 10.2 [b]	5 ± 2.7 [b]	60 ± 35.6 [a]	57 ± 13.3 [a]
Chilopoda	64 ± 26.2 [a]	10 ± 4.7 [b]	2 ± 1.6 [b]	15 ± 5.9	52 ± 28.1	10 ± 6.3
Coleoptera (Adults)	25 ± 10.3 [a]	35 ± 5.7 [a]	0 [b]	16 ± 7.0	21 ± 10.0	22 ± 8.1
Coleoptera (Larvae)	42 ± 15.8	121 ± 29.7	30 ± 10.5	58 ± 23.0	94 ± 30.9	41 ± 13.5
Diplopoda	19 ± 5.6 [a]	17 ± 6.7 [a]	0 [b]	6 ± 4.2	12 ± 5.1	17 ± 7.2
Diptera (Larvae)	331 ± 209.7	185 ± 33.6	127 ± 39.3	141 ± 44.3	264 ± 210.8	238 ± 44.1
Gastropoda	1 ± 1.2	1 ± 1.2	1 ± 1.2	1 ± 1.2	0	2 ± 1.6
Hemiptera	60 ± 34.4	535 ± 390.3	610 ± 240.7	217 ± 87.1	86 ± 31.5	901 ± 420.9
Hymenoptera	4 ± 1.9 [c]	10 ± 2.9 [b]	36 ± 12.1 [a]	14 ± 5.8	9 ± 3.6	27 ± 12.7
Formicidae	47 ± 46.9	1 ± 1.2	0	47 ± 46.9	0	1 ± 1.2
Lumbricidae	185 ± 73.3	19 ± 6.9	32 ± 12.1	11 ± 6.1	78 ± 54.3	147 ± 59.8
Total macrofauna	925 ± 318.6	1180 ± 410.8	1026 ± 326.4	625 ± 146.8	826 ± 306.8	1680 ± 432.2

significantly greater at Skulow Lake than Log Lake ($F_{2,26}$=14.97, p=0.0002 and $F_{2,26}$=4.77, p=0.022, respectively). Relative abundance of Coleoptera larvae also differed among sites ($F_{2,26}$=6.58, p=0.007), however, specific differences among sites could not be assigned. Proportions of Coleoptera adults ($F_{2,26}$=18.86, p=0.00004) and Diplopoda ($F_{2,26}$=4.38, p=0.028) were higher at Log Lake and Topley than at Skulow Lake (see Table 3.1). Relative abundance of Hemiptera ($F_{2,26}$=14.97, p=0.0002) differed among all three sites, being highest at Skulow Lake followed by Topley and then Log Lake.

Generally, densities of most macrofaunal taxa increased from spring to fall, however these differences were not significant. Only densities of pseudoscorpions differed significantly among seasons ($F_{2,26}$=13.70, p=0.0002) with higher densities during fall and summer than spring (Table 3.1). Relative abundances of three taxa differed significantly among seasons (Figure 3.3b). Coleoptera larvae represented a greater proportion of the macrofauna in summer than fall ($F_{2,26}$=5.51, p=0.014). Relative abundance of Chilopoda decreased ($F_{2,26}$=5.37, p=0.015) and that of Lumbricidae increased ($F_{2,26}$=5.58, p=0.013) from spring to fall.

Figure 3.3. Comparison of relative abundance of soil macrofauna among (a) sites and (b) seasons. Bold type indicates significant differences. See text for statistics.



3.3.2 Short-term treatment impact

Overall, density of total soil macrofauna was significantly lower in whole tree harvest/light compaction (OM2C1) and stem-only harvest/heavy compaction (OM1C2) plots than in uncut forest control plots (OM0C0) (Figure 3.4). Densities of four major taxa also differed significantly among treatments (Table 3.2). Densities of Hemiptera and Chilopoda were significantly lower in stem-only/heavy compaction plot than in uncut forest control or stem-only/no compaction plots (OM1C0). Densities of Pseudoscorpionida were significantly lower in stem only/heavy compaction plots than in the other three plots. Density of this taxon was also significantly lower in the whole tree/light compaction plots than in the uncut forest control. Densities of Diplopoda also differed significantly among treatments with substantially lower densities in whole tree/light compaction plots than the other three plots. Although stem-only harvesting reduced densities of all macrofauna taxa (to 4% to 80% of control levels, see Table 3.2), reductions were not statistically significant.

Overall, structure of the macrofauna community differed only slightly among the four treatments with relative abundance of Hemiptera, Chilopoda and Pseudoscorpionida differing significantly among treatments (Figure 3.5). Relative abundance of these three taxa was significantly lower in stem-only/heavy compaction plots than in uncut forest control plots, similar to the pattern presented in Table 3.2. Relative abundance of pseudoscorpions was

Figure 3.4. Comparison of mean density (+SE) of total macrofauna among treatments. Columns with same letter are not significantly different.

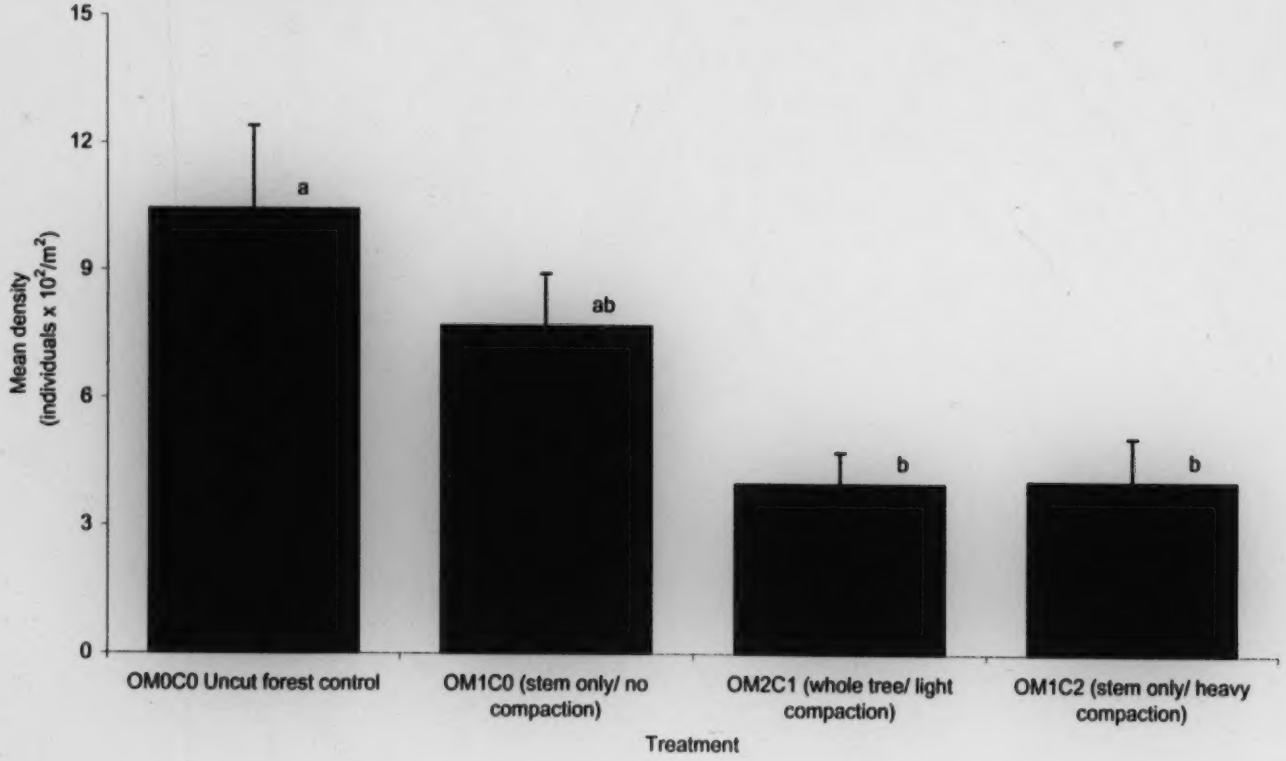
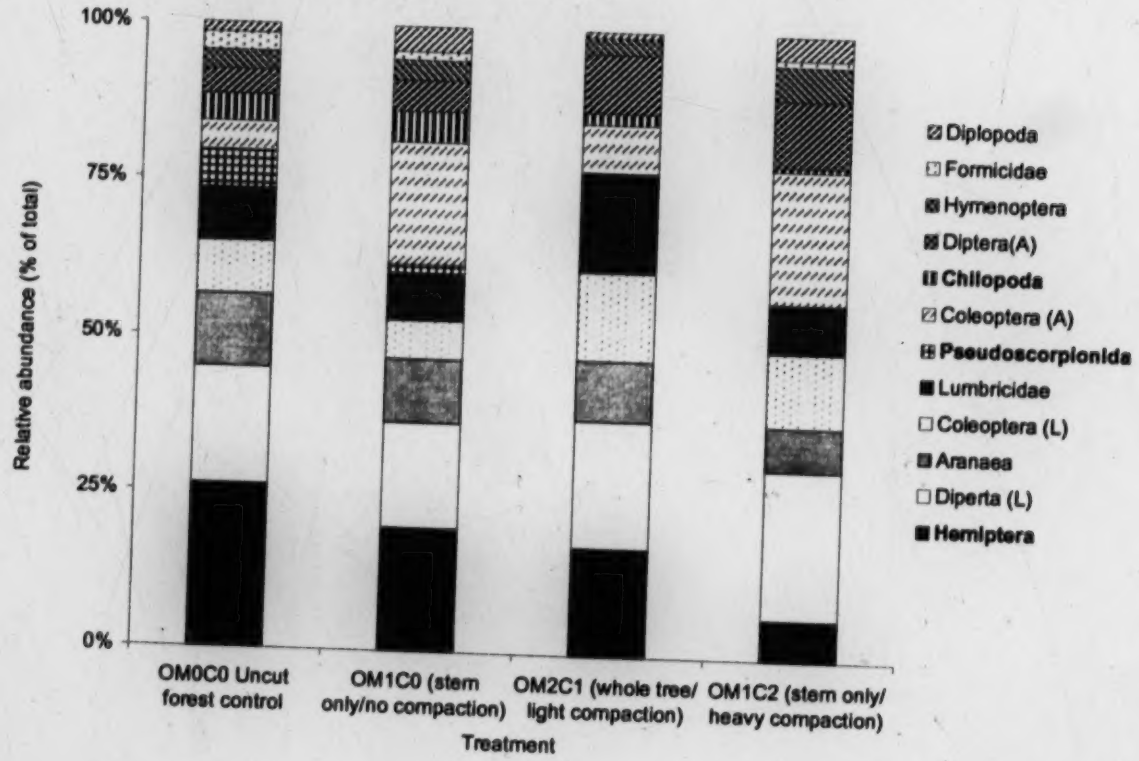


Table 3.2. Comparison of mean density (individuals/m^2) (± SE) of macrofauna among treatment plots. Data pooled from all three sites. 'A' indicates ANOVA, 'np' indicates non-parametric analysis using ranked scores. Values followed by a blank or same letter not significantly different (Tukey's test or non parametric comparison of means. α=0.05. Asteriks indicate significant differences among means when comparison of means failed to detct differences (* $p<0.05$).

		OM0-C0		OM1-C0		OM2-C1		OM1-C2	
Aranaea		96 ± 22		52 ± 12		39 ± 23		20 ± 7	
Pseudoscorpionida	np	41 ± 13	a	9 ± 4	ab	1 ± 1	b	0 ± 0	c
Chilopoda	np	26 ± 10	a	16 ± 5	a	5 ± 2	ab	2 ± 1	b
Coleoptera (Adult)	np	20 ± 5		151 ± 77		19 ± 8		151 ± 93	
Coleoptera (Larvae)		64 ± 14		23 ± 6		36 ± 8		42 ± 13	
Diplopoda	np	12 ± 3	*	12 ± 4	*	1 ± 1	*	8 ± 4	*
Diptera (Adult)		24 ± 7		38 ± 10		27 ± 9		25 ± 6	
Diperta (Larvae)		214 ± 71		112 ± 27		77 ± 17		63 ± 14	
Hemiptera	A	402 ± 155	a	189 ± 74	a	71 ± 21	ab	21 ± 10	b
Hymenoptera	np	16 ± 5		27 ± 9		7 ± 2		15 ± 6	
Formicidae	np	16 ± 16		5 ± 2		0 ± 0		1 ± 1	
Lumbricidae		79 ± 28		50 ± 17		83 ± 30		22 ± 8	

Figure 3.5. Comparison of relative abundance (% of total) of macrofauna among treatments. Bold type indicates significant difference. See text for statistics.



also significantly lower in whole tree/light compaction plots than in the uncut forest control plots (Figure 3.5). This suggests that compaction, when combined with tree harvesting has a greater influence on density and structure of the soil macrofauna community than tree harvest alone.

3.4 Discussion

3.4.1 Comparison among subzones

Climate and soil chemical and physical properties differed among sites as well as density and structure of the soil macrofaunal community, even when identified at class and order level.

Climates of the study sites covered the range of climatic conditions within sub-boreal spruce forests from cold and moist at Topley to dry and warm at Skulow Lake (see Chapter 2). Climate may also influence seasonal changes in density or structure of soil macrofauna. In the present study, densities of macrofauna were higher during fall and spring than summer. Seasonal changes in soil fauna densities have been documented previously. The highest population densities generally occur during spring and fall in most temperate forest soils (Wallwork 1976, Edwards 1991). These population peaks may be related to root growth and associated rhizosphere activity during spring and organic matter input during fall, both of which would provide food resources for faunal reproduction and activity (McCoy 1990). Warmer temperatures at Skulow

Lake may also allow plant activity to start earlier and last longer than at Log Lake and Topley which could influence herbivore activity (McCoy 1990).

Differences in elevation among sites may also influence the distribution of soil fauna. Topley and Skulow Lake are higher in elevation (1100 m and 1050 m, respectively) than Log Lake (750 m). McCoy (1990) suggested that species density and richness would be higher at mid-elevations than at lower elevations due to a higher net accumulation of photosynthate at mid elevations, which creates a larger resource base for herbivores and their predators.

Chemical and physical properties of soils varied significantly among all three sites. In general, chemical concentrations in both the forest floor and mineral soil at Skulow Lake were consistently lower than Log Lake or Topley except for magnesium and pH (see Table 2.3). Soil nutrients influence the distribution of fungi and can indirectly affect the distribution and density of soil arthropods (Setälä et al. 1995). Since soil macrofauna feed on fungi, or other fungivores, the amount or quality of fungal biomass available would influence their density and distribution as well as increase competition among soil fauna for those resources.

In the present study, pH was significantly higher at Skulow Lake than at either Log Lake or Topley. Fecal material, with a higher pH, can counteract acid conditions found in mor humus forms (Wallwork, 1970). Langmaid (1964) observed an increase in pH on one study site because of lumbricid activity. Although lumbricid densities were higher at Log Lake, species richness was greater at Skulow Lake. In the present study, two earthworm species were

identified. Dendrobaena octaedra (Savigny) was collected at all threes sites but Lumbricus rubellus Hoffmeister was collected only at Skulow Lake. Both species are considered epigeic, occupying upper litter layers and consuming principally surface litter (MacLean et al. 1996, Zhang and Hendrix 1995). Lumbricus rubellus is generally larger than D. octaedra, 50 to 150 mm vs. 17 to 60 mm (Reynolds 1977), and probably contributes more to organic matter breakdown. Furthermore, L. rubellus has a wider habitat tolerance than D. octaedra and can live below the soil surface or in the litter layer year round and aggregates beneath dung in pastures (Reynolds 1977).

Fender (1985) suggested that most worm species belonging to the family Lumbricidae are introduced from Europe. Cattle present in the forests at Skulow Lake could transport these worms into new habitats in soil and organic debris collected in the animal's hooves. Sport fishing at Skulow Lake near the study site may also be responsible for introducing L. rubellus since this species is cultivated by the fish bait industry (Reynolds 1977).

Increased earthworm activity could raise soil pH and alter soil structure, which could change microbial activity and alter the composition of soil fauna. For example, Loranger et al. (1998) found significantly higher densities of Collembola associated with higher densities of the earthworm Polypheretima elongata (Megascolicidae) in 15-year-old pastures in Martinique. They related this correlation to earthworm activity increasing food resources and pore distribution and enhancing soil structure.

Quality and quantity of the litter layer can also play a role in the distribution of soil organisms (Schaeffer and Schauermann 1990). In the present study, significant differences in forest floor and mineral soil physical properties were observed among all three sites (see Table 2.3). For example, forest floor mass (4.1 kg/m^2), bulk density (82 kg/m^3) and depth (5.2 cm) were all significantly lower at Skulow Lake than at Log Lake (7.6 kg/m^2, 114 kg/m^3, 6.6 cm) or Topley (7.8 kg/m^2, 112 kg/m^3, 7.1 cm). The thicker forest floor at Topley may present a greater variety of habitats and more food resources, resulting in higher densities at Topley. One would therefore expect lower densities at Skulow Lake than Log Lake, since the former has a thinner forest floor. However, this was not the case in the present survey. In fact, densities of soil macrofauna were more similar between Topley and Skulow Lake.

In the present study, densities of predatory groups, such as spiders, pseudoscorpions, centipedes and ants differed among sites. High spider and low ant densities were observed at both Topley and Skulow Lake while a high density of ants, pseudoscorpions and centipedes and low density of spiders were observed at Log Lake. This pattern may indicate some type of interaction among these predatory groups. Ants exert a strong influence on ecosystem function (Kajak et al. 1972). Thus, spider density could be related to ant foraging activity (Petal and Breymeyer 1969). Various studies have shown that high ant densities were associated with decreased spider numbers (Petal and Breymeyer 1969, Kajak et al. 1972, Cherix and Bourne 1980), however other studies have found no significant correlation between spider and ant densities (Van der Aart and de

Wit 1971, Brüning 1991). In the present study, only a weak negative correlation between ant and pseudoscorpion densities was significant among sites.

Different humus forms are characterized by different groups of soil animals. For example, macrofauna are more abundant in mull soils while mesofauna are dominant in moder and mor soils (Wallwork 1970, Schaeffer and Schauermann 1990). Both L. rubellus and D. octaedra are acid-tolerant and can be found in mor soils (Wallwork, 1970). The humus form at Skulow Lake is considered a moder-type while those at Topley and Log Lake have been classified as hemimor humus forms (see Table 2.1). The presence of L. rubellus at Skulow Lake may be responsible for the differences in humus forms and forest floor depth between these sites. Huhta et al. (1967) suggested that L. rubellus contributed to moder humus formation at one study site. MacLean et al. (1996) found entire F and H horizons replaced by worm casts of D. octaedra in Pinus contorta forests in southwestern Alberta. Over a period of three years, lumbricid activity in virgin podzol soils of Atlantic Canada completely changed the upper organic horizons into a single, uniform horizon consisting mostly of earthworm casts covered by a thin litter layer (Langmaid 1964). Increased activity by large detritivores such as earthworms and diplopods would increase the total rate of energy turnover, enhancing productivity in the soil ecosystem (Wallwork 1970). However, the long-term impact of changes to various soil chemical and physical properties, as well as on soil fauna populations, nutrient cycling and decomposition rates because of earthworm activity in coniferous forests are unknown at this time but deserve further study.

3.4.2 Short-term treatment impact

Different soil fauna groups respond to habitat disturbance in a variety of ways, depending upon how soil chemical and physical properties or soil climate change. In the present study, soil chemistry did not differ significantly among treatments. With soil physical properties, only bulk density in the mineral soil increased significantly because of soil compaction (see Chapter 2). Changes to soil climate after harvesting include: 1) increased light to the soil surface; 2) changes to soil moisture; and 3) extreme temperature fluctuation in the exposed area (Huhta et al. 1967).

Heat sum values, calculated for six of the nine treatment plots at each site from September 20, 1996 to September 20, 1997, were higher on those plots with higher compaction and more organic matter removal (Kranabetter and Chapman 1999) suggesting greater temperature fluctuations on these plots. In fact, soil temperatures were colder during winter and warmer during summer on plots where the forest floor and slash had been removed compared to those plots still covered by forest floor and slash (see Figures2.6-7). Freeze/thaw events occurred more frequently on plots with whole tree harvest and forest floor removed than stem only or whole tree harvested plots (M. Kranabetter, unpublished results). Downward movement in the organic horizon by soil macrofauna would be limited due to the significantly higher bulk density in the mineral soil (see Chapter 2). Thus, macrofauna that might normally over-winter

deeper in the organic horizon would be exposed to colder temperatures in the forest litter, increasing mortality and reducing densities of macrofauna.

Generally, densities of most macrofauna taxa in this study decreased significantly as treatment severity increased. Densities of most macrofauna taxa in the stem only harvested/no compaction plots did not differ significantly from the uncut control plots. However, the combination of tree harvest and soil compaction had a greater impact on densities than did tree harvest alone. Whole-tree harvesting combined with light compaction or stem only harvesting with heavy compaction reduced the density of total macrofauna by more than 50% in the short-term while densities in the stem-only harvested plots were only about 25% less than the control. In a hardwood forest at the LTSPS installation in Missouri, Jordan et al. (1999) found that heavy soil compaction significantly reduced earthworm biomass and density the first year after treatment application.

Although densities of macrofauna decreased with harvesting and soil compaction, relative abundance for most taxa remained unchanged in this study. Huhta et al. (1967) also reported no conspicuous changes in relative abundance among macrofauna after clear-cutting. Greenberg and McGrane (1996) also reported no significant changes in total biomass or abundance of macrofauna among burn/salvage, clear-cut/site preparation, clear-cut/seeded or mature (control) forests. This indicates that, in the short-term, whole tree and stem only harvesting combined with soil compaction had little impact on the overall structure of the soil macrofauna community at higher taxon levels on the present

study sites. However, further analysis at the species level may show profound changes in community structure and should be considered in future.

Soil macrofauna may respond more slowly to disturbance. For example, David et al. (1991) examined the impact of litter interception and increased litter supply on macrofauna populations in an oak forest in France. They found no significant decreases in densities before one year in lumbricids, two years in isopods and zoophagous Diptera larvae, and two and half years in diplopods, saprophagous Diptera larvae and chilopods. Thus, treatment impacts on soil macrofauna at these LTSPS sites may not be observable until two years or later after treatment.

Continued monitoring of the LTSP sites will provide valuable information on the long-term changes to the soil macrofauna community after soil compaction and organic matter removal as well as enhance basic knowledge on the structure and diversity of soil macrofauna community in these sub-boreal forests. Although the higher-level taxa results presented in this study showed a limited response by macrofauna, it provides baseline samples and data for further investigations at genus or species levels provided interest and funding are available.

Incorporating biological data with physical and chemical data will aid in the development of guidelines for ecologically beneficial harvesting practices. These practices would aim to limit disturbance and removal of organic matter and soil compaction in order to maintain the integrity and structure of the soil macrofauna community, which will enhance long-term sustainability of forest soils.

3.5 Literature Cited

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Chapter 4: Comparison of soil mesofauna and oribatid mite species among three different subzones of the Sub-Boreal Spruce Zone in central British Columbia.

4.1 Introduction

Soil mesofauna includes those organisms ranging in size from 0.1 to 2 mm in body width (Swift et al. 1979). Hundreds of species, represented by thousands or millions of individuals, can occupy a single square meter of soil (Moldenke 1990, Battigelli et al. 1994). Mites (Acari) and springtails (Collembola) dominate the mesofauna numerically. Other taxa in this group include Protura, Diplura and Symphyla as well as smaller sized species of Diplopoda, Chilopoda, Araneae, enchytraeid worms and pseudoscorpions (Swift et al. 1979).

Mesofauna play a variety of functional roles in soil processes and contribute to the maintenance of soil fertility (Seastedt 1984). They influence bacterial and fungal biomass via grazing, liberating immobilized nutrients and stimulating further fungal and bacterial activity as well as enhancing plant growth (Parkinson 1988, Setälä 1995). Furthermore, soil mesofauna transport microbial propagules and spores into new substrates (Kethley 1990, Norton 1990) and contribute to the development of soil structure and humus formation through the deposition of fecal pellets (Pawluk 1985, Hendrix et al. 1990). Soil fauna activity is also used in soil humus classifications (Green et al. 1993) and precise identification of species could characterize different soil types (Rusek 1989). These organisms may also function as bioindicators of changes in soil health or quality (Wallwork

1988, Hogervorst et al. 1993, Linden et al. 1994, Pankhurst et al. 1995, van Straalen and Verhoff 1997).

Oribatida (or Cryptostigmata) are one of the most abundant taxa of soil arthropods (Wallwork 1983, Norton 1990) with densities reaching several hundred thousand individuals per square meter in the organic horizon (Petersen and Luxton 1982, Battigelli et al. 1994). Approximately 7,000 species have been described worldwide, representing more than 1000 genera belonging to more than 150 families (Balogh and Balogh 1992) and all are closely tied to soil habitats (Norton 1990, Behan-Pelletier 1999).

Oribatid mites are long-lived, with low metabolic rates and slow development times (Norton 1990). Although this inhibits their ability to take advantage of rapid changes in food resources, low metabolic rates enable them to survive periods with low food intake (Mitchell 1977). Oribatid species have developed various reproductive strategies. Iteroparity, repeated reproduction by the same female, is common among oribatid mites (Norton 1990). Certain oribatid species living in the litter layer oviposit throughout the year while those species in the fermentation or humus zones reproduce seasonally, usually ovipositing in the spring or summer (Mitchell 1977). These factors result in a considerable overlap of generations producing relatively stable population densities in most undisturbed soils.

Members of some oribatid families, such as Eremaeidae, Camisiidae, Oppiidae and Tectocepheidae, are thelytokous where by all reproduction is parthenogenetic and males are absent (Perrot-Minnot and Norton 1997). As a

reproductive strategy, thelytoky provides members of these families with great colonization abilities in disturbed habitats. This is especially important given that most oribatid species are poor dispersers (Siepel 1996). With these attributes, oribatid mites would be useful as biological indicators in terrestrial ecosystems (Wallwork 1983, Behan-Pelletier 1999).

Unfortunately, distribution of soil fauna in Canadian soils is poorly known. Only 53% of the estimated 48,500 species of soil arthropods in North America have been described (Behan-Pelletier and Bissett 1992). Furthermore, <25% of the Canadian oribatid fauna is known at the species level and basic information on distribution, ecology, life history and functional roles for most species is also limited (Behan-Pelletier 1993). Information regarding the density, diversity and distribution of soil fauna is essential if one is to use this community as biological indictors of soil health and to monitor changes in disturbed ecosystems (Behan-Pelletier 1999).

Previous studies of soil fauna communities in British Columbia have been limited to southern coniferous forests. At present, there is no specific knowledge of the density, distribution, diversity or function of soil fauna in the Sub-Boreal Spruce (SBS) biogeoclimatic zone and this is the first study to examine the biodiversity of soil fauna within the SBS of central British Columbia. There are two specific objectives for this chapter. First, to document the density and distribution of the soil mesofauna community, in general, and the diversity of oribatid mite species, in particular, from the organic and mineral soil among three different subzones of the SBS in central British Columbia. Second, to explore

relationships between these two groups and selected physcio-chemical properties of the soils at these sites.

4.2 Materials and Methods

4.2.1 Study sites

This study was conducted within the Sub-Boreal Spruce (SBS) zone in the central interior of British Columbia (Figure 2.1). Refer to Chapter 2 for further information on site descriptions, plot layout and treatment application at the three replicate installations of the Long Term Soil Productivity Study.

4.2.2 Sampling, sorting and identification of soil mesofauna

Three 3.0 X 3.0 m plots, > 10 m apart, were randomly located in uncut forest (> 1 ha in size) adjacent (~500-750 m in distance) to the LTSPS treatment areas at each site and subdivided into 36 subplots (0.5 X 0.5 m) (see Figure 2.1). All plots at each site were sampled in the same phenological windows for two years (1992 and 1994 at Topley and Log Lake; and 1993 and 1995 at Skulow Lake). Timing of sample collection was based on: bud burst on trembling aspen (spring); soil temperature of 10 ^{o}C at 10 cm (summer) and leaf colour change in trembling aspen (fall). In addition to standardizing sampling times among sites, these indicators relate to biological activity in the soil and span the range of seasonal variation in distribution and life stages for soil fauna at these sites.

For each sampling date, one soil core (4.5 cm in diameter) was removed from each of three randomly selected subplots at each site (large rocks and downed logs were avoided). The top 3 cm from both organic and mineral soil horizons was removed from each core. Each subplot was sampled only once during the study to limit the impact of soil removal and habitat alteration.

Within 48 hours of collection, samples were placed in a modified high-gradient extractor for one week (Lussenhop 1971). Data loggers were used to monitor temperature changes during extraction. Mesofauna were collected into a 0.6% (w/v) picric acid solution and then transferred into 1-dram glass shell vials with 70% ethanol by washing the contents of the collecting dishes with distilled water through a 50 µm sieve until no picric acid remained.

All samples were initially sorted and counted under a dissecting microscope. Collembola were identified to family, and Acari to suborder. Within the samples, several taxa, other than Acari and Collembola, occurred at very low densities. These were pooled into one group, hereafter referred to "Other mesofauna". All mesofauna samples are stored with the B.C. Ministry of Forests Research Branch Laboratory, P.O. Box 9536 Victoria, B.C. V8W 9C4.

Oribatid specimens were sorted to morphospecies under a dissecting microscope, cleared with lactic acid, temporarily mounted on cavity slides and identified to species under a compound microscope (Norton 1990). Identifications were carried out using Balogh and Balogh (1992), Norton (1990, 1992), Balogh and Mahunka (1983) as well as other species keys and original species descriptions. Dr. Valerie Behan-Pelletier (Agriculture Canada Eastern

Cereal and Oilseed Research Centre, Ottawa) confirmed species identifications. Classification of oribatid species follows Marshall et al. (1987). Number of individuals per taxon was recorded for each sample. Voucher specimens will be deposited with Biodiversity Assessment and Evaluation Research Branch, Agriculture Canada Eastern Cereal and Oilseed Research Centre, K.W. Neatby Building, Central Experimental Farm, Ottawa, Ontario K1A 0C6.

Soil chemical properties, including total carbon, total nitrogen, C/N ratio, mineralizable nitrogen, total phosphorous, total sulphur and pH, were determined from the soil cores used for soil mesofauna extraction. Organic soil samples were milled in a hammer mill. Mineral soil samples were crushed with a rolling pin to break up agglomerates and then screened through a 2mm sieve. Total nitrogen, carbon were measured using a Leco CHN-600 Elemental Analyzer and total sulphur was measured using a Leco Sulphur Determinator SC132, all via combustion. Mineralizable nitrogen was determined by anaerobic incubation and measured colorimetrically using a Technicon Auto-analyzer II. Available phosphorus was determined using the Bray P1 Phosphate method and measured by absorbance at 882.0 nm on a Milton Roy Spectronic 1201 spectrophotometer with autosampler. Data collection for both methods was Labtronics DP1000. Soil pH was determined in water. Methods follow those outlined by Kalra and Maynard (1991) and Carter (1993). Depth of the forest floor, consisting of L, F and H horizons, was measured when each core was removed.

4.2.3 Data analyses

Density (number of individuals/sample) and relative abundance ([number of individuals per taxon/total individuals collected] x 100) were used in the analyses. Density is useful for estimating population size and determining changes in absolute abundance while relative abundance is useful to compare distribution patterns of taxa and the similarity of these patterns among sites, seasons or horizons (Wallwork 1976).

Only taxa with an overall relative abundance $\geq$1% of all collected material were considered for further analyses. Data were transformed to meet assumptions of normality before analyses. Density data were log transformed [$\log_{10}$ (X+1) where X = actual count of individuals/sample for a taxon] and relative abundance data were arcsine transformed (arcsin$\sqrt{p}$ where p=relative abundance of the taxon).

A 3-way ANOVA [site x season x horizon (3 x 3 x 2)] with years pooled was used to analyze mesofauna density and relative abundance data. A non-parametric test of ranked scores was used for those taxa that did not have normally distributed data (SAS 1990). Statistical significance was judged using the Type III F test for both procedures. If significant differences were found among main factors using ANOVA, then Tukey's Studentized range test was used to specify significant comparisons. A Tukey-type multiple comparison test was used in conjunction with the non-parametric test results (Zar 1984).

Using oribatid mite species data, three diversity indices, the exponential form of Shannon-Wiener Index (N_1) (Hill 1973), the reciprocal of Simpson's Index

(N_2) (Hill 1973) and the modified Hill's ratio for evenness (E) (Ludwig and Reynolds 1988) as well as the average number of species/sample were calculated for each sample (see Appendix A for equations). N_1 measures the number of very abundant species and is sensitive to changes in rare species abundance. It represents the number of equally common species required to generate the observed heterogeneity. N_2 measures the number of abundant species and is sensitive to changes in abundant species. Values for N_2 represent the number of equally common species that would produce the same diversity as the Shannon-Wiener Index (Magurran 1988). Higher values for both indices indicate greater diversity. Units for N_2 and N_1 are number of species and thus more easily interpreted than the Shannon-Wiener Index (Hill 1973). The modified Hill's ratio examines the evenness (E) of species distribution in a community and indicates increased dominance of a single species as the value of E approaches zero (Ludwig and Reynolds 1988). Diversity values were analyzed using a 3-way ANOVA [site x season x horizon (3 x 3 x 2) - years pooled].

The Morisita-Horn index (C_λ) was calculated, using EstimateS Version 5.0.1 (Colwell, 1997), to examine the similarity of the oribatid species assemblage among sites and years (seasons pooled) for both the mineral and organic horizons, respectively. Cluster analysis was performed on the resulting similarity matrices using Unweighted Arithmetic Averaging (Krebs 1989). Dendrograms were constructed to interpret cluster analysis results.

Species accumulation curves for oribatid mite assemblages were estimated using rarefaction. Rarefaction compensates for differences in sampling effort (in this case, the number of individuals collected) and estimates the number of species expected in a random sample of individuals drawn from a collection (Krebs 1989).

Spearman Correlation analysis (r_S) by horizon, followed by a sequential Bonferroni test (Rice 1989), was performed among selected soil properties and densities of soil mesofauna and oribatid species. Linear regression (r) was performed with forest floor depth and densities of soil mesofauna and oribatid species and diversity values.

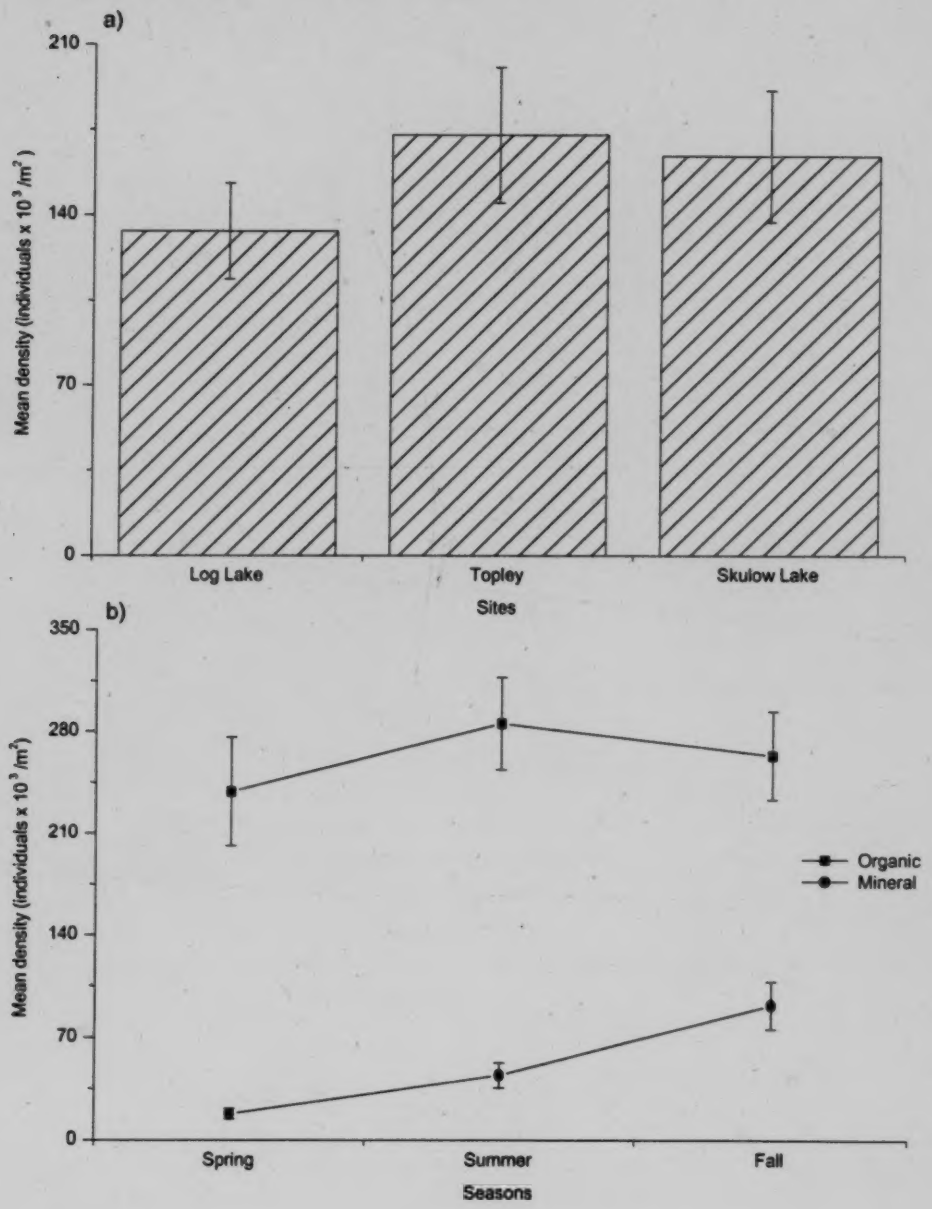
Density (number of individuals/m^2) and relative abundance (% of total) are reported as mean ± standard error, unless stated otherwise. The SAS package (SAS Institute 1990) was used for all statistical tests in this study with α=0.05.

4.3 Results

4.3.1 Soil mesofauna

Mean density of total soil mesofauna did not differ significantly among sites (Figure 4.1a). However, there was a significant season by horizon interaction ($F_{2,107}$=9.47, p=0.0001). Densities in the organic horizon did not differ significantly among seasons; however, densities of total soil mesofauna in the mineral soil increased from spring to fall (Figure 4.1b).

Figure 4.1. Comparison of mean density of total soil mesofauna (±SE) (a) among sites and (b) with significant season by horizon interaction.



Densities of only two taxa differed significantly among sites. Isotomidae were most abundant at Topley ($F_{2,107}$=4.78, p<0.05) and the mean density of Oribatida was lowest ($F_{2,107}$=6.38, p<0.005) at Log Lake (Table 4.1). Mean density of Astigmata was significantly lower in fall than either spring or summer ($F_{2,113}$=3.8, p<0.05). Mean density of Hypogastruridae also differed significantly among seasons ($F_{2,107}$=3.44, p<0.05); however, Tukey's test failed to detect any differences. There was also a significant site by horizon interaction for both mean density ($F_{2,107}$=9.4, p=0.0002) and relative abundance ($F_{2,107}$=9.4, p=0.0002) of Hypogastruridae. This was probably in response to a single, large catch of hypogastrurids in the organic horizon at Skulow Lake during summer (see Table 4.1). Densities of most taxa were higher in the organic horizon than the mineral soil. However, only densities of Onychiuridae, total Collembola and Astigmata were significantly higher in the organic than mineral horizon ($F_{1,107}$=15.68, p<0.0005; $F_{1,107}$=80.25, p<0.0005; and $F_{1,113}$=13.50, p<0.0005 respectively) (Table 4.1).

Both density and relative abundance values of several taxa had significant interactions. Densities of Mesostigmata were higher in the organic horizon at Topley, did not differ significantly among sites in the mineral soil ($F_{2,107}$=4.67, p=0.012) (Figure 4.2a). There was also a significant season by horizon interaction for mean density of Mesostigmata ($F_{2,107}$=4.9, p=0.01) (Figure 4.2b), Oribatida ($F_{2,107}$=5.57, p=0.005), Prostigmata ($F_{2,107}$=8.18, p=0.0001) and total Acari ($F_{2,107}$=9.47, p=0.0001) (Figures 4.3 a, b and c, respectively). In all four cases, the pattern was similar to the season by horizon interaction for total soil

Table 4.1. Comparison of mean density (individuals x $10^3/m^2$) (± SE) of mesofauna among a) sites, b) seasons and c) horizons using ANOVA (A) or non-parametric analysis (np) using rank scores. Blanks for analysis indicate analysis not done. Values followed by a blank or same letter not significantly different (Tukey's test or non-parametric comparison of means. α=0.05. Asterisks indicate indicate significant differences among means when comparison of means failed to detct differences (* p<0.05, ***p<0.0005).

		a) SITES			b) SEASONS			c) HORIZONS	
		Log Lake	Topley	Skulow Lake	Spring	Summer	Fall	Organic	Mineral
Entomobryidae		0.4 ± 0.20	0.2 ± 0.09	0.5 ± 0.20	0.3 ± 0.18	0.5 ± 0.18	0.3 ± 0.14	0.7 ± 0.19	0.03 ± 0.020
Hypogastruridae	np	4.8 ± 1.70	3.3 ± 0.80	18.0 ± 16.29	2.2 ± 0.75 *	18.9 ± 16.28 *	4.9 ± 1.64 *	15.8 ± 10.86	1.5 ± 0.52
Isotomidae	np	6.3 ± 1.62 *	18.7 ± 6.33 *	6.6 ± 1.47 *	12.4 ± 6.27	7.8 ± 1.49	11.3 ± 2.41	19.0 ± 4.26	2.0 ± 0.39
Neelidae		0.5 ± 0.28	0.5 ± 0.25	1.4 ± 1.31	0.1 ± 0.11	0.2 ± 0.08	2.1 ± 1.33	1.6 ± 0.89	0.05 ± 0.023
Onychiuridae	A	4.8 ± 1.24	12.6 ± 3.83	6.3 ± 1.13	7.1 ± 3.02	5.8 ± 1.20	10.8 ± 2.75	12.1 ± 2.60 **	3.7 ± 0.85 ***
Sminthuridae		0.6 ± 0.51	0.2 ± 0.07	0.1 ± 0.07	0.8 ± 0.50	0.1 ± 0.03	0.1 ± 0.07	0.6 ± 0.34	0.03 ± 0.020
Tomoceridae		0.2 ± 0.07	0.1 ± 0.06	0.8 ± 0.37	0.3 ± 0.11	0.2 ± 0.09	0.6 ± 0.36	0.7 ± 0.25	0.03 ± 0.026
Total Collembola	A	18.4 ± 3.26	36.8 ± 8.31	35.4 ± 16.81	23.7 ± 7.73	35.3 ± 16.62	31.6 ± 5.49	52.3 ± 11.91 *	8.1 ± 1.34 *
Oribatida	A	29.9 ± 5.53 a	55.5 ± 11.09 b	56.1 ± 11.92 b	44.6 ± 11.41	43.4 ± 9.22	53.1 ± 9.74	77.2 ± 9.21	17.0 ± 3.88
Mesostigmata	A	6.6 ± 1.17	9.0 ± 1.61	5.2 ± 0.86	7.2 ± 1.49	6.6 ± 1.14	7.0 ± 1.18	12.1 ± 1.03	1.8 ± 0.32
Prostigmata	A	74.9 ± 13.02	64.7 ± 9.73	61.3 ± 12.12	45.2 ± 9.36	73.9 ± 13.41	81.9 ± 11.20	112.0 ± 9.22	22.0 ± 4.56
Astigmata	A	0.6 ±0.18	3.4 ±1.14	3.0 ±0.97	3.4 ±1.26 a	3.4 ±0.89 a	0.7 ±0.36 b	3.7 ±0.90 a	1.1 ±0.49 b
Total Acari	A	112.1 ± 17.14	132.6 ± 20.22	125.6 ± 20.07	100.3 ± 19.34	127.3 ± 19.60	142.7 ± 18.09	204.9 ± 13.97	41.9 ± 6.60
Other mesofauna		2.8 ± 0.81	3.4 ± 1.00	3.2 ± 0.71	4.2 ± 1.26	2.0 ± 0.36	3.2 ± 0.62	5.1 ± 0.87	1.2 ± 0.23

Figure 4.2. Mean density of Mesostigmata with significant (a) site by horizon and (b) season by horizon interactions.

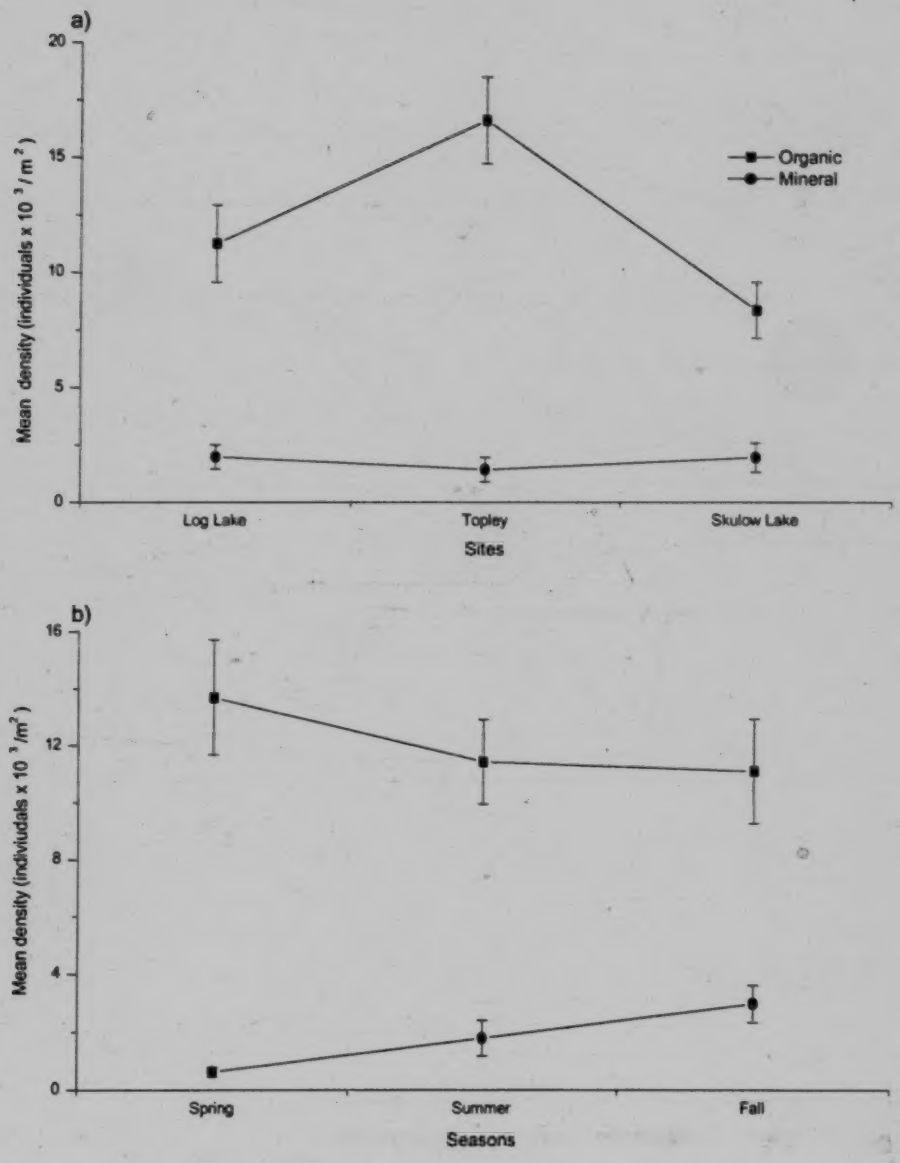
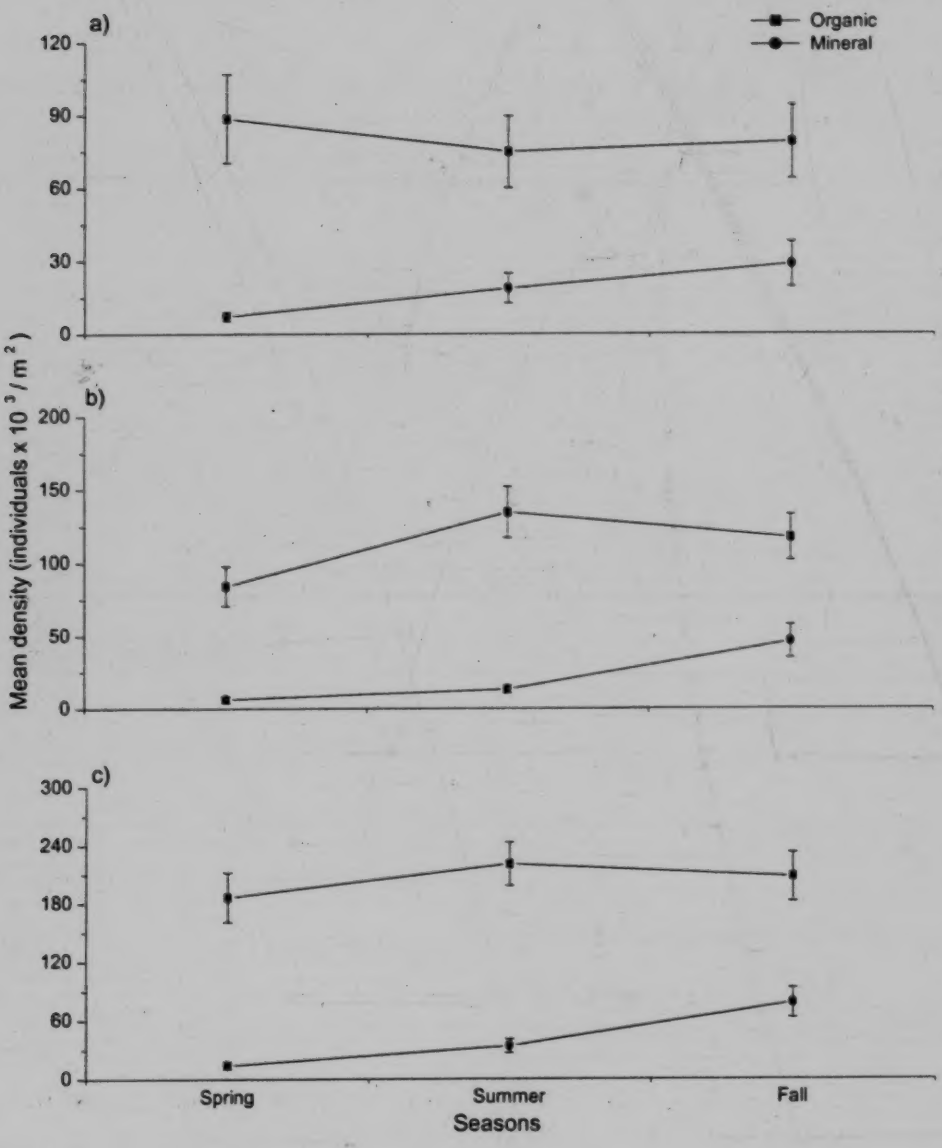


Figure 4.3. Significant season by horizon interaction for densites of (a) Oribatida, (b) Prostigmata and (c) total Acari.

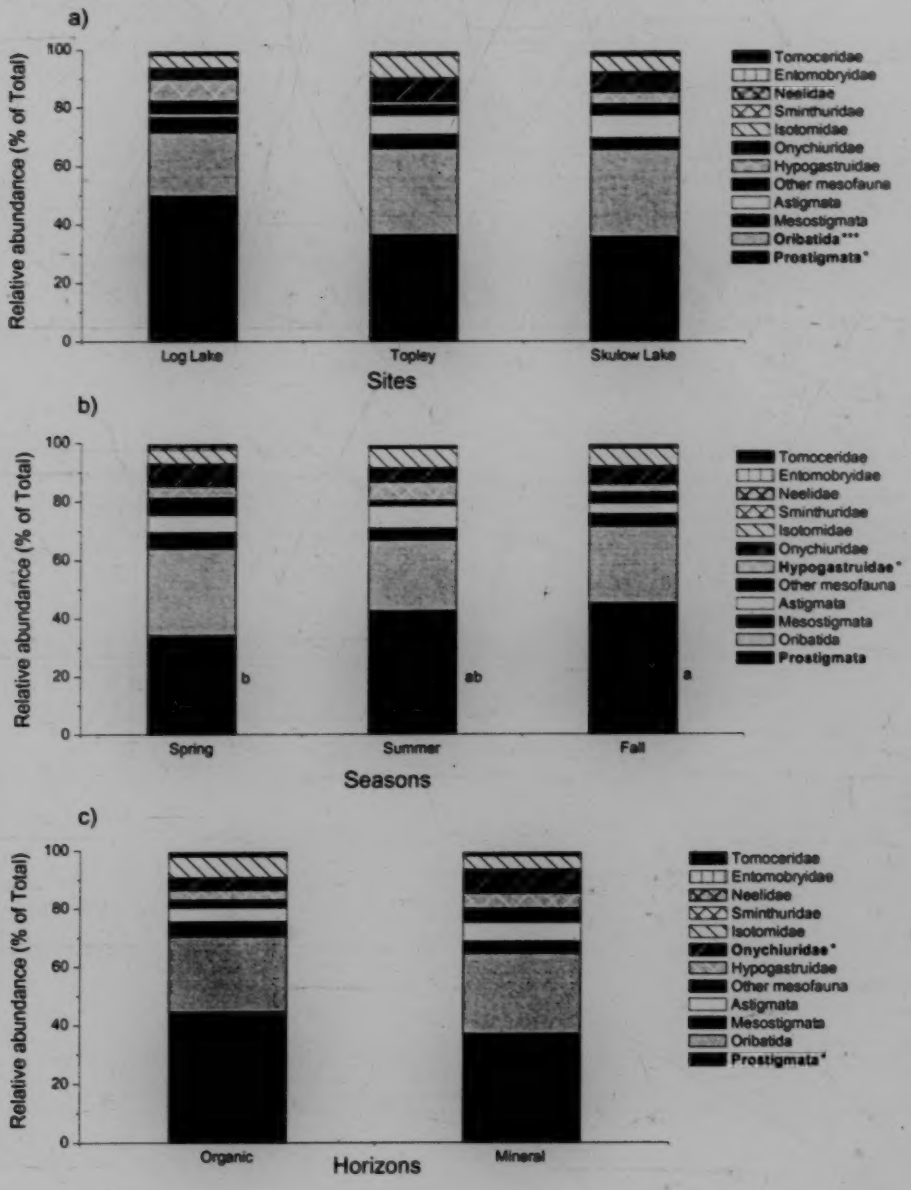


mesofauna density (see Figure 4.1b) with no significant difference among the organic horizons and an increase in density from spring to fall in the mineral soil.

Structure of the mesofauna community, based on relative abundance data, was similar across all sites, seasons and horizons. Acari accounted for approximately 75-80% of the mesofauna collected while Collembola represented 15-20% with other mesofauna contributing a few percent (0-5%). Prostigmata and Oribatida were the dominant acarine taxa and Isotomidae, Hypogastruridae and Onychiuridae were dominant collembolan taxa (Figures 4.4a, b, and c). Relative abundance of Oribatida was lowest ($F_{2,107}$=7.33, $p<0.0005$) and that of Prostigmata highest ($F_{2,107}$=5.08, $p<0.05$) at Log Lake (Figure 4.4a).

Relative abundance of both Hypogastruridae and total Collembola differed significantly among seasons ($F_{2,107}$=3.44, $p<0.05$ and $F_{2,107}$=4.60, $p<0.05$, respectively) but Tukey's test failed to detect differences between any pairs of means (Figure 4.4b). Relative abundance of Prostigmata was significantly higher in the fall than spring ($F_{2,107}$=3.52, $p<0.05$) (Figure 4.4b) and higher in the organic horizon than in the mineral soil ($F_{2,107}$=4.23, $p<0.05$) (Figure 4.4c). Relative abundance of Onychiuridae was significantly higher in the mineral soil than in the organic horizon ($F_{2,107}$=4.18, $p<0.05$) (Figure 4.4c).

Figure 4.4. Comparison of relative abundance of soil mesofauna (% of total) among (a) sites, (b) seasons and (c) horizons. Means followed by blank or same letter are not significantly different according to Tukey's test (α=0.05). Asterisks indicate significant difference among means (* p<0.05, ***p<0.0005).



4.3.2 Oribatid mites

Eighty-nine species in 45 genera from 26 families were identified from just over 7,000 individuals. Forty-five species are new records for British Columbia and 11 species are new records for Canada (see Appendix B). Most oribatid species found at these sites are distributed broadly in the Northern Hemisphere. Of the 49 taxa identified to described species, 31 species (65%) were Holarctic, 14 species (29%) were Nearctic and 3 (6%) were cosmopolitan.

Diversity and density of the oribatid fauna was greater in the organic horizon than in the mineral. In the organic horizon, both species richness and rate of species accumulation of oribatid mites were higher at Skulow Lake (N_0=60) than either Topley (N_0=48) or Log Lake (N_0=36) (Figure 4.5a). In the mineral soil, species richness was similar among all three sites even though rate of species accumulation of oribatid mite species was greater at Log Lake than Skulow Lake or Topley (Figure 4.5b).

Diversity measures did not differ significantly among seasons. However, all three values (N_2, N_1 and E) had significant site by horizon interactions ($F_{2,113}$=5.04, p=0.001; $F_{2,113}$=9.05, p=0.0003; and $F_{2,113}$=9.05, p=0.0003, respectively) (Figure 4.6). Values for N_2 and N_1 indicated greater diversity of oribatid mite species in the organic horizon than in the mineral soil at both Topley and Skulow Lake; the reverse was true at Log Lake (Figures 4.6a and b, respectively). Low diversity values in the organic horizon at Log Lake reflect the high numerical dominance of Oppiella nova (Oudemanns 1902) (68%).

Figure 4.5. Rate of oribatid mite species accumulation using rarefaction for the (a) organic horizon and (b) mineral soil.

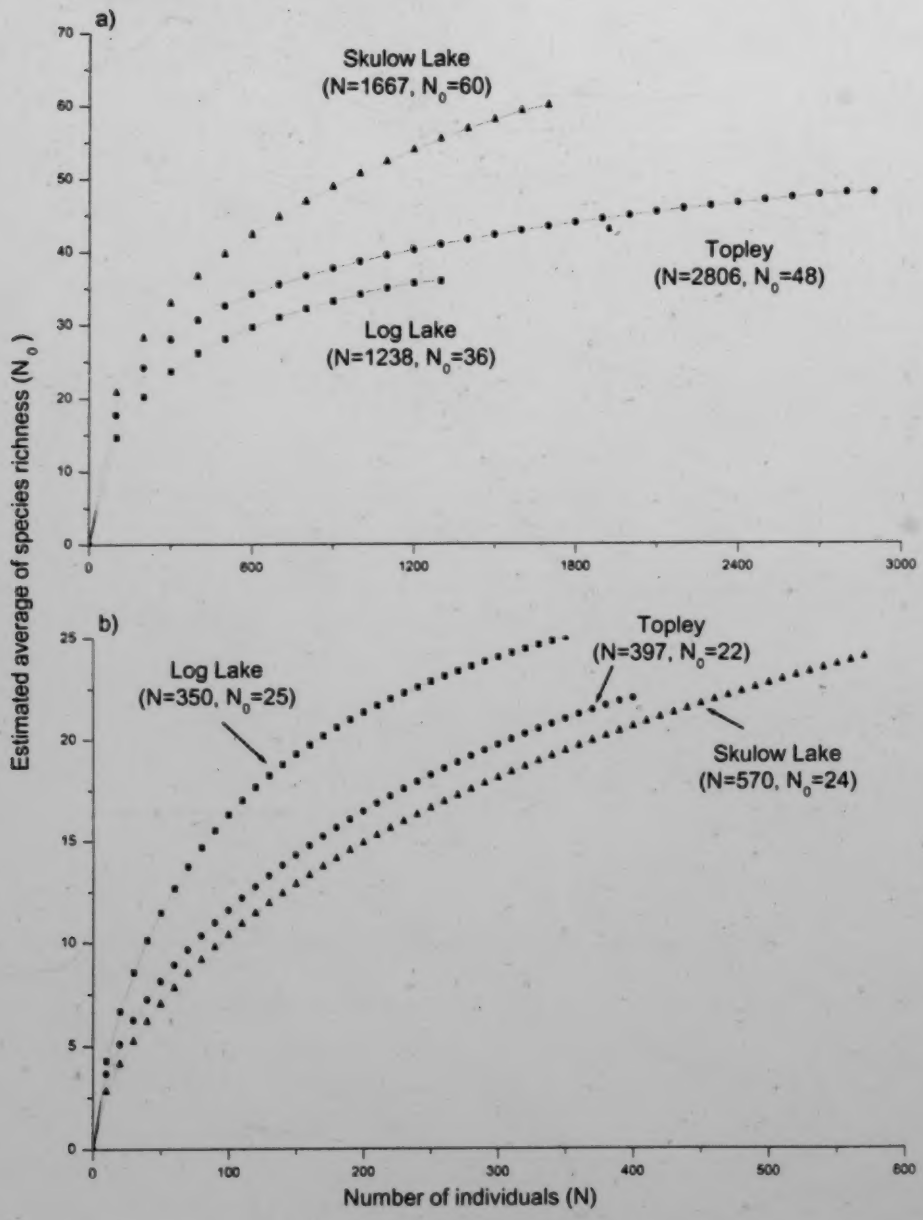


Figure 4.6. Significant site by horizon interactions for (a) Reciprocal of Simpson's Index (N_2), (b) Exponential of Shannon-Wiener Index (N_1), and (c) Evenness (E).

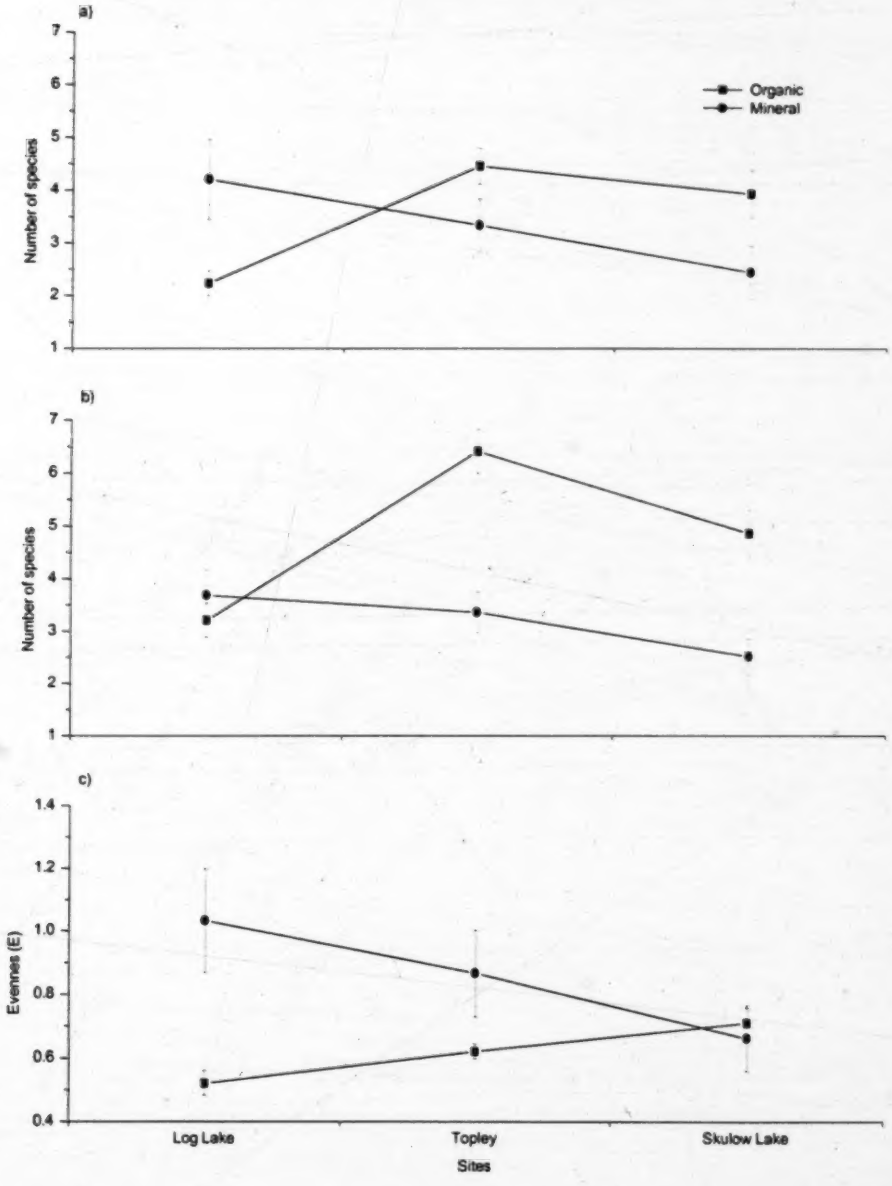


Table 4.2. Percent representation (% of total oribatid specimens) of the most common species (> 3%) at each site in each horizon (seasons pooled) arranged from most common to least.

	Log Lake		Skulow Lake		Topley	
	organic	mineral	organic	mineral	organic	mineral
Oppiella nova	68.2	47.5	48.2	59.2	40.8	22.9
Moritzoppia clavigera					16.0	40.2
Suctobelbella sp.nr. acutidens	*	9.9	7.2	7.4	13.5	4.2
Ceratozetes thienemanni	*	9.0	*		*	5.5
Scheloribates sp.1			*	8.5	*	
Suctobelbella sp.3	5.7	*	*		*	*
Tectocpheus velatus			5.7	*	*	
Sellnickochthonius suecica	4.1	5.4	*			*
Suctobelbella sp.7	*	5.1			*	*
Brachychthonius sp.	*	*	*	4.9	*	*
Jornadia n.sp.			4.6	*		
Heminothrus longisetosus			*	*	3.9	
Oppia sp. 1			3.7			
Multioppia sp.			3.4	*	*	
Suctobelbella sp. 6	*	*	*	*	3.3	*

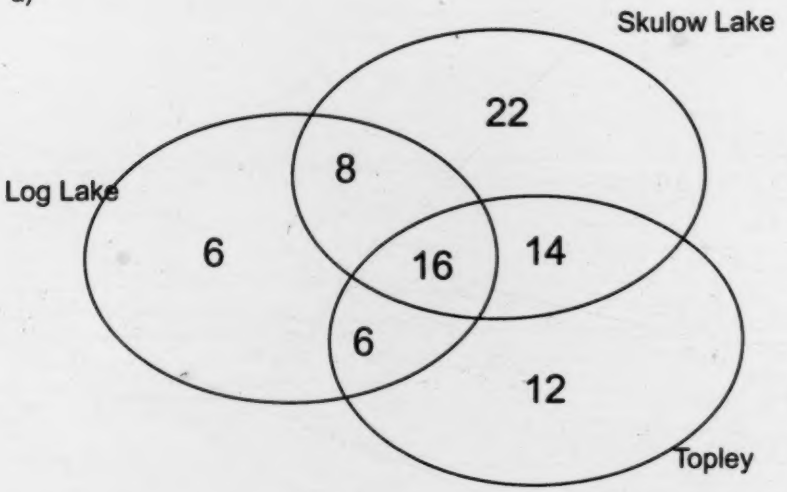
* represented by less than 3%. Blank cell indicates species not present.

Evenness (E) in the mineral soil decreased from Log Lake to Skulow Lake while the reverse was true in the organic horizon although on a much smaller scale (Figure 4.6c). Higher evenness is reflected in the steepness of the rarefaction curves in Figures 4.5. The steepest rarefaction curve in the mineral soil was for Log Lake (Figure 4.5b), which also had the highest evenness. In the organic horizon, Skulow Lake had the steepest curve (Figure 4.5a) as well as the highest evenness.

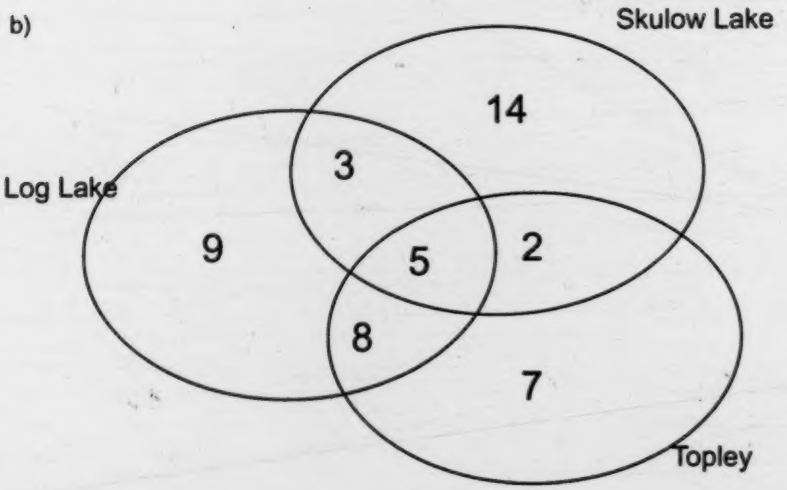
Most species were represented by few individuals while several common species accounted for >50% of the individuals collected (Table 4.2, Appendix B). O. nova was the most abundant species at all three sites in both the organic horizon and mineral soil except in the mineral soil at Topley where Moritzoppia clavigera (Hammer, 1952) was the most abundant species (Table 4.2). The numbers of species unique in both the organic and mineral soil at Skulow Lake (22 and 14, respectively) were higher than either Topley (12 and 7) or Log Lake (6 and 9) (Figures 4.7 a and b). Only a few individuals represented the majority of unique species. However, several species, unique to a single site were present in large numbers. For example, one new species, from the genus Jornadia, was collected only at Skulow Lake in both mineral and organic soils (see Chapter 5). Moritzoppia clavigera, at Topley, and Oppia sp.1, at Skulow Lake, represent other unique species with high densities at specific sites (Table 4.2). Sixteen species were common at all three sites (see Figure 4.7a and b and Appendix B).

Figure 4.7. Number of oribatid species common among Log Lake, Skulow Lake and Topley in the a) organic horizon and b) mineral soil.

a)



b)



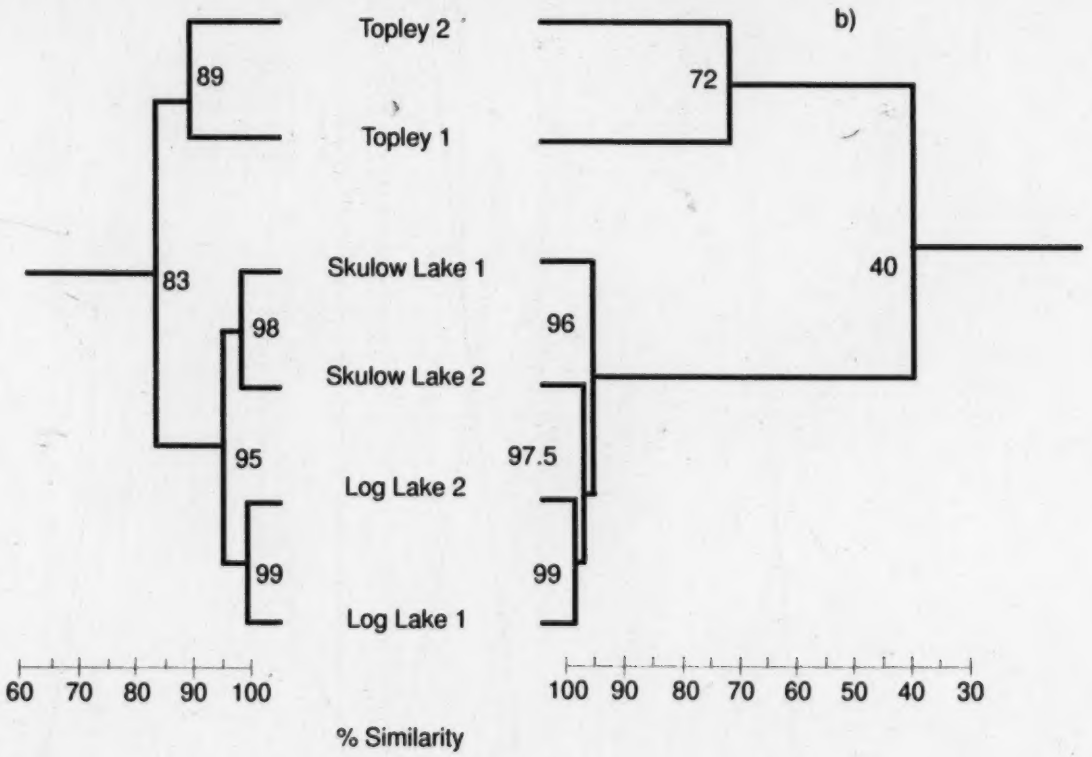
Dendrograms, constructed using the Morisita-Horn similarity index, indicated that assemblages of oribatid mite species were similar among sites in both the organic horizon and the mineral soil (Figure 4.8). In the organic horizon, the oribatid species assemblage was 83% similar among all three sites. Similarity of the species assemblages was higher still within each site. In the mineral soil, the oribatid species assemblage was 96% similar between Log Lake and Skulow Lake but only 40% similar between these 2 sites and Topley. This was most likely influenced by different dominant species in the mineral soil among the sites (see Table 4.2).

4.3.3 Soil fauna and soil properties

4.3.3.1 Soil Mesofauna

In the organic horizon, densities of three mesofaunal taxa had significant, but weak, positive correlations to several soil chemical properties: Hypogastruridae with C:N ratio (r_s=0.39, p=0.003); Prostigmata with total nitrogen (r_s=0.39, p=0.003); and Mesostigmata with phosphorus (r_s=0.37, p=0.006) and total carbon (r_s=0.37 p=0.006). In the mineral soil, density of Isotomidae had a significant positive correlation with total carbon (r_s=0.36, p=0.009) and sulphur (r_s=0.44, p=0.003).

Figure 4.8. Cluster analysis of Morisita-Horn index using oribatid species by sites and years (1=first year, 2=second year) from the (a) organic horizon and (b) mineral soil with node values presented.



Forest floor depth was positively correlated with densities of Isotomidae, Oribatida, Mesostigmata, Prostigmata, Astigmata, Total Acari and Total mesofauna in the organic horizon. There were no significant correlations in the mineral soil (Table 4.3). For the combined data (organic plus mineral), densities of Isotomidae, Astigmata, total Acari and total mesofauna were positively correlated with forest floor depth (Table 4.3).

4.3.3.2 Oribatid mites

Spearmann Rank Correlation analysis showed significant correlations between several oribatid mite species and soil chemical data. In the organic horizon, there were small, significant, positive correlations between total carbon and densities of Ceratozetes thienemanni (r_s=0.42, p=0.002), M. clavigera (r_s=0.36, p=0.009) and Suctobelbella sp.6 (r_s=0.43, p=0.001). Densities of M. clavigera (r_s=0.48, p=0.0003), Suctobelbella sp.6 (r_s=0.41, p=0.002) and Suctobelbella sp.nr. acutidens (r_s=0.44, p=0.001) were positively correlated with phosphorus. S. sp.nr. acutidens (r_s=0.41, p=0.003) was also positively correlated with C:N ratio. Densities of Jornadia n.sp. were negatively correlated with total carbon (r_s= -0.37, p=0.007) and total nitrogen (r_s= -0.40, p=0.003).

Densities of O. nova, S. sp.nr. acutidens, and Suctobelbella sp.6 from the organic horizon and combined data were positively correlated with forest floor depth (Table 4.4). Density of M. clavigera from the combined data was also positively correlated to forest floor depth (Table 4.4). Number of species (N_0) in

Table 4.3. Regression coefficients (r) from analysis of density of mesofauna against forest floor depth. Asterisks indicate significant correlation (*p<0.05, **p<0.005).

	Organic	Mineral	Combined
Entomobryidae	0.22	-0.18	ns
Hypogastruridae	-0.07	-0.03	ns
Isotomidae	0.38**	-0.03	0.37**
Neelidae	-0.013	0.1	ns
Onychiuridae	0.25	0.05	ns
Sminthuridae	0.05	0.003	ns
Tomoceridae	-0.17	-0.12	ns
Total Collembola	0.12	0.03	ns
Oribatida	0.28*	-0.1	ns
Mesostigmata	0.3*	-0.012	ns
Prostigmata	0.29*	-0.15	ns
Astigmata	0.4**	-0.03	0.33*
Total Acari	0.4**	-0.17	0.28*
Other mesofauna	0.23	-0.15	ns
Total mesofauna	0.38**	-0.15	0.28*

Table 4.4. Regression coefficients (r) of abundance of dominant oribatid species against forest floor depth. Asterisk indicates significant correlation (*p<0.05).

	Organic	Mineral	Combined
Sellnickochthonius suecia	-0.03	-0.02	ns
Ceratozetes thienemanni	0.24	-0.05	ns
Jornadia n.sp.	-0.06	-0.05	ns
Scheloribates sp.1	-0.17	0.11	ns
Moritzoppia clavgiera	0.26	-0.23	0.28*
Oppiella nova	0.31*	-0.13	0.27*
Suctobelbella sp.6	0.32*	-0.1	0.27*
Suctobelbella sp.nr. acutidens	0.28*	-0.08	0.28*
Tectocepheus velatus	-0.09	0.01	ns

ns=not significant

the organic horizon was also positively correlated with forest floor depth ($r=0.43$, $p<0.005$). There were no significant correlations between species richness in the mineral horizon and selected chemical properties or forest floor depth.

4.4 Discussion

In the present study, densities of soil mesofauna ranged from several hundred to several hundred thousand individuals per square meter at each study site. These values compare well with other published data. For example, densities of Collembola in this study ranged from 19 - 37 x $10^3/m^2$, which are similar to collembolan densities reported from an old growth spruce stand in Finland (20 - 45 x $10^3/m^2$) (Huhta et al. 1967). Densities of total Acari in this study (112 - 132 x $10^3/m^2$) were lower than those reported from Finnish conifer forests (274 x $10^3/m^2$) (Huhta et al. 1967) or Canadian Pseudotsuga plantations (206 x $10^3/m^2$) (Marshall 1974). Densities of Oribatida (30 - 60 x $10^3/m^2$) were similar to those reported from a Netherlands pine forest (3 - 100 x $10^3/m^2$) (Hogervorst et al. 1993, Teuben and Smidt 1992) and mixed oak stands in North Carolina (44.2 x $10^3/m^2$) (Lamoncha and Crossley 1998). However, higher densities of oribatids have been observed in old-growth spruce stands in Finland (75 - 200 x $10^3/m^2$) (Huhta et al. 1967) and mature mixed conifer/hardwood stands in Delhi, Ontario (74 x $10^3/m^2$) (Tomlin and Miller 1987). Densities of Prostigmata in the present study (60 - 75 x $10^3/m^2$) were within the range for woodland habitats (0 - 210 x $10^3/m^2$) (Petersen and Luxton 1982).

Structure of the mesofauna community was consistent across all sites, seasons and horizons in the present study. Acari were the dominant group, representing about 78% of the total mesofauna. Collembola represented approximately 18% of the mesofauna with various other mesofaunal taxa representing the remaining few percent. Similar proportions for these broad mesofaunal groups have been observed in other forest soil ecosystems including a mixed hardwood stand in North Carolina (Lamoncha and Crossley 1998) and in spruce forest soils (Bornebusch 1930 as cited by Wallwork 1970).

Oribatid mites are generally the most abundant mites in the soil (Wallwork 1970). A cursory study of organic horizons in temperate forests should uncover 30 to 50 oribatid species (Norton 1990). The total number of species identified in this study, 89 among all three sites, is comparable to oribatid species richness in other studies. For example, 73 species were identified from old growth balsam fir (Abies balsamea (L.)) forests in Newfoundland (Dwyer et al. 1998), more than 60 dominant species were found in the coniferous biome of the Pacific Northwest (Moldenke and Fichter 1988) and 47-61 species from spruce (Picea glehni Mast.) forests in Japan (Fujikawa 1974). The number of species in litter and soil of southeastern Appalachian forests ranged from 64-96 along an elevational gradient (Lamoncha and Crossley 1998). Oribatid species richness in the present study was also similar to tropical litter (63 species) and soil (27 species) systems (Behan-Pelletier et al. 1993).

In the present study, 45 new oribatid species were recorded for British Columbia, doubling the number of species previously recorded in the province

(43 [Behan-Pelletier 1993]). Furthermore, 11 species were recorded for the first time in Canada. There were numerous species unique to each site, the most being at Skulow Lake. However, most of these species were rare with relative abundances <1% of the total oribatid fauna. Exceptions included Jornadia n.sp. and Tectocepheus velatus, both found only at Skulow Lake. I identified 55% of the oribatid taxa to described species, even though <25% of the Canadian oribatid fauna are known at the species level (Behan-Pelletier 1993). The majority of oribatid species identified in the present study are broadly distributed in the Northern Hemisphere (65% were Holarctic and 29% were Nearctic). The wide northern distribution of these species combined with reliable taxonomical surveys of oribatid mite species from northern European forests provides greater resolution of identified species (Behan-Pelletier 1999).

Density and diversity of mesofauna were significantly higher in the organic horizon than in the mineral soil, with more than 80% of the total mesofauna and twice the number of oribatid species in the organic horizon compared to the mineral soil. It is generally recognized that the majority of soil organisms are found in the organic horizon, with densities and diversity decreasing with depth (Wallwork 1970, Price 1973, Price 1975, Petersen and Luxton 1982, Battigelli et al. 1994). The organic horizon provides a more diverse habitat than the mineral soil due to larger pore spaces and a greater variety of food resources (Hågvar, 1983).

Oribatid mite species diversity has been positively correlated to microhabitat diversity in woodland forest soils (Anderson 1978). Quality and

quantity of the litter layer can also influence the distribution and density of soil organisms (Schaeffer and Schauermann 1990, Blair et al. 1994). Mor humus forms, similar to the hemimor humus forms found at both Topley and Log Lake, provide greater habitat diversity due to a larger standing crop of litter and the presence of stratified litter layers (Teuben and Smidt 1992), resulting in higher densities and greater diversity of mesofauna. Since Skulow Lake had a moder-type humus form with a thinner forest floor than the other two sites, lower densities and diversity of mesofauna might be expected at this site; however, this was not the case. The thicker forest floor at Topley provides a great diversity of habitats, which may account for the greater number of oribatids collected at this site. However, overall species richness was greater at Skulow Lake, which had a thinner forest floor as well as a lower bulk density than the other two sites. In fact, densities of soil mesofauna were more similar between Topley and Skulow Lake and oribatid species diversity was substantially higher in the organic horizon at Skulow Lake than Topley or Log Lake. Species richness in the mineral soil at all three sites was relatively poor with 24-27 species recorded, similar to tropical soil systems (Behan-Pelletier 1993).

Generally, soil chemistry has limited direct effect on the density and diversity of soil mesofauna since bodies of most soil mesofauna are hydrophobic (Hågvar and Abrahamsen 1984). However, soil nutrients can have an indirect effect on soil arthropods by influencing the distribution of fungi (Setälä et al. 1995). Since soil mesofauna, in general, and oribatid mites, in particular, feed

on fungi, the amount or quality of fungal biomass available can influence their density and distribution.

In the present study, densities of Prostigmata, Oribatida and Mesostigmata were affected by significant season by horizon interactions. Although seasonal shifts in vertical distribution of soil mesofauna can be difficult to observe (Schenker 1984), several studies have demonstrated seasonal migration of Collembola and Acari within the soil profile (Usher 1970, 1971, Marshall 1974). Densities of all three acarine suborders were higher in the organic horizon than in the mineral soil during all seasons. Generally, densities in the organic horizon did not differ significantly among seasons. However, in the mineral soil, densities of these acarine suborders increased from spring to fall. This differs from the seasonal pattern of high spring and fall densities is observed in most temperate forest soils (Wallwork 1976, Edwards 1991). Peaks in density during autumn and winter with lower densities during summer are closely correlated to reproductive cycle of soil animals (Wallwork1970). Seasonal changes alter the soil environment, affecting soil temperature, soil moisture content, organic matter input, root growth as well as fungal and bacterial activity, which also influence soil fauna activity. During spring, reduced root growth and rhizosphere activity could limit faunal activity and population growth. Increased organic matter input through the summer and fall, coupled with root activity and senescence, may positively affect food resources thereby increasing faunal activity and reproduction of certain taxa.

Haarløv (1960) suggested that most soil microarthropods reproduce only when ecological factors permit. Collembola and certain species of Prostigmata respond more rapidly to changes in food supply and reproduce at higher rates. Other species of Prostigmata and Oribatida are not able to do so (Kethley 1990, Norton 1990). Low metabolic and feeding rates coupled with increased longevity and iteroparity among oribatids may result in a more stable population and reduce seasonal and annual fluctuations in densities in undisturbed sites (Norton 1990). Increased densities in the mineral soil during autumn may reflect an increase in the number of juvenile forms present. These smaller forms inhabit the mineral soil since the smaller pore space would provide protection from predators and climatic fluctuations and limit competition from larger adult forms (Wallwork 1970).

Climates also differed considerably among sites. Log Lake was considered the wettest, Topley the coldest and Skulow Lake the warmest and driest. These differences may also influence distribution and diversity of oribatid mite species among sites. For example, drier, warmer conditions at Skulow Lake may influence the presence of Jornadia n.sp. This genus includes two other species that are also found in drier habitats: J. larreae Wallwork and Weems 1984 is found in the Chihuahuan desert of North America (Wallwork and Weems 1984); and J. longipilis Pérez-Iñgio and Baggio 1991 is described from São Paulo State in Brazil (Pérez-Iñgio and Baggio 1991). The cold, wet climate at Topley may favour the presence of Moritzoppia clavigera. This species has a Holarctic distribution (Colloff and Seyd 1991) and the genus has been found in

Newfoundland on sites influenced by a boreal maritime climate with short, cool summers and cold, snowy winters (Dwyer et al. 1998) similar to the climate at the Topley site.

The warmer climate at Skulow Lake may also allow earlier faunal activity in spring. However, drier conditions at Skulow Lake may also restrict activity by limiting water resources later in the summer. Soil moisture content can influence the distribution of soil organisms (Price 1975, Metz 1971). However, Berthet and Gerard (1965) found no correlation between Acari numbers and soil water content when soils were at "normal" water content (25-90%). Furthermore, Price (1975) suggested that most undisturbed forest habitats maintain soil moisture contents throughout the year that meet the requirements of soil fauna.

Since most classes and orders of soil organisms are widely distributed (Anderson 1977), one would expect little difference among sites in this study at family/suborder level of identification. Indeed, density of total soil mesofauna did not differ significantly among sites. However, densities of Isotomidae, Oribatida and Prostigmata did. A large, single collection of isotomids at Topley during 1992 (230×10^3 individuals/m^2) most likely explains the significant difference in density of this collembolan family among sites. Both density and relative abundance of oribatid and prostigmatid mites were similar between Topley and Skulow Lake (approximately 60,000/m^2 and 35%, respectively). At Log Lake, however, density and relative abundance of Prostigmata were more than twice those of Oribatida (75,000 vs. 30,000/m^2 and 50% vs. 23%, respectively). Fewer

oribatid species were collected at Log Lake (36 species) than at either Topley (48 species) or Skulow Lake (60 species).

Different elevations among sites may influence species richness due to changes in litter decomposition rates or lower temperatures at higher elevations (Lamoncha and Crossley 1998). In the present study, oribatid species richness and site elevation (780-790 m) were lowest at Log Lake. Species richness and elevation were higher at both Topley (1100 m) and Skulow Lake (1050 m). These results are similar to those presented by Lamoncha and Crossley (1998) who found higher oribatid diversity with increasing elevation. However, one might expect similar species richness at both Skulow Lake and Topley since these two sites have similar elevations. The warmer climate at Skulow Lake may enhance the habitat and permit a greater diversity of oribatid species than at the colder climate at Topley.

Similarity in species assemblages of the organic horizons was near 83% among all three sites. However, in the mineral soil, there was greater similarity between oribatid assemblages of Log Lake and Skulow Lake (96%) than with the oribatid assemblage at Topley (40%). This difference among sites was related to a different dominant species in the mineral soil at Topley (Moritzoppia clavigera) compared to Skulow Lake and Log Lake (Oppiella nova).

Differences in proportions of oribatid and prostigmatid mites at Log Lake could indicate an earlier disturbance at this site. The Log Lake site is near a high-tension power line and tire tracks are visible in the forest. Diversity values of both N_1 and N_2 were lower for the organic horizon at Log Lake than either

Topley or Skulow Lake. An abundance of rare species can influence diversity indices, as can the dominance of a single species (Ludwig and Reynolds 1988). O. nova was very abundant at Log Lake, representing nearly 70% of the oribatid fauna. In other studies, Oppiella spp. accounted for <20% of the oribatid fauna (Lamoncha and Crossley 1998) and O. washburni (Hammer 1952) represented 20-35% of the oribatid fauna (Dwyer et al. 1998). The dominance of O. nova may be further indication of some earlier disturbance at this site. This species is parthenogenetic and has a long life span. Coupled with a high fecundity rate and diverse feeding habits, O. nova is able to rapidly occupy a diverse range of habitats in large numbers (Ryabinin and Pan'kov 1987). Greater densities or proportions of species from families such as Brachychthoniidae, Tectocepheidae and Oppiidae, to which O. nova belongs, can indicate a recent disturbance (Behan-Pelletier 1999).

Density, diversity and structure of the oribatid mite community differed among the three subzones examined in this study. Differences in the composition of the oribatid species assemblages among sites, in addition to several oribatid species being restricted to a single site, supports the use of oribatid fauna as biological indicators of different forest soil types. Ecosystem classification in British Columbia incorporates climate, soil and vegetation data (Pojar et al. 1991), which are products of climate, organisms, topography, parent material and time (Major 1951). Identification of different subzones at each study site reflects differences in climate and vegetation on a large scale. The small size, great diversity and sensitivity to environmental variability of soil fauna

can also reflect habitat heterogeneity and environmental stress (Weaver 1995) on both small and large scales and a over a shorter time period than vegetation such as trees. However, for soil fauna to become a more significant part of ecosystem classification, a better understanding of their function, activity, distribution and life history is required.

Soil fauna communities at these sites are not influenced by any single climatic factor or chemical or physical soil property measured in this study. The interaction of numerous abiotic and biotic soil properties and climatic factors may have greater influence on the distribution and diversity of soil mesofauna and oribatid mite species than any single factor (Anderson 1977, Fjellberg 1985).

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4.6 Appendices

Appendix A. Equations

Evenness calculation (Hill 1973, Ludwig and Reynolds 1988):

$$E = \frac{N_2 - 1}{N_1 - 1}$$

E approaches 0 as a single species becomes more dominant in a community.

Shannon-Wienner Function (Magurran 1988):

$$H' = -\Sigma\, p_i \ln p_i$$

where p_i = the proportional abundance of the i^{th} species.

Exponential form of Shannon-Wienner function (Hill 1973):

$$N_1 = e^{H'}$$

where e=2.71828

H' = Shannon-Wienner function (calculated with base e log (LN))

N_1 = number of equally common species which would produce the same diversity as H'.

Reciprocal of Simpson's Index (Hill 1973, Magurran 1988):

$$N_2 = 1/D$$

where $D = \Sigma \frac{(n_i (n_i - 1))}{(N(N-1))}$

where n_i = the number of individuals in the i^{th} species, and N = the total number of individuals.

The value of this index increases with increasing diversity.

Appendix B. List of oribatid mite species and their abundance (years and replicates pooled, n=6) collected at each site from the organic horizon/mineral soil during three seasons. Distribution patterns area as follows: C=cosmopolitan; H=Holarctic; N=Nearctic; n=Neotropical; P=Palearctic;O=Oriental; S=Subantarctic; A=Australian.

		Distribution	LOG LAKE fall	spring	summer	TOTAL	SKULOW LAKE fall	spring	summer	TOTAL	TOPLEY fall	spring	summer	TOTAL	OVERALL TOTAL
Palaeosomata															
Palaeacaridae															
Palaeacarus hystricinus*	Tragardh, 1932	H		2/	/2	2/2	1/1	42/		43/1	19/2	/1	5/	24/3	69/6
Enarthronota															
Atopochthoniidae															
Atopochthonius auriodactylus*	Grandjean, 1948	H	2/	6/	/1	8/1	1/10	13/1		14/11					22/12
Brachychthoniidae															
Brachychthonius bimaculatus	Willmann,1936	H					/1	/1		/2					/2
sp.				6/	/2	6/2	1/1	1/1		2/2		/1	2/	2/1	28/5
Eobrachychthonius borealis*	Forsslund, 1942	H		1/	/4	1/4							23/1	23/1	24/5
latior*	(Berlese, 1910)	H									5/	5/	7/	17/	17/
Liochthonius brevis*	(Michael, 1888)	H/A						3/		3/	3/			3/	6/
muscorum**	Forsslund, 1964	P/O			1/	1/		1/	/2	1/2	2/	3/	1/	15/	17/2
simplex**	(Forsslund, 1942)	P	1/	4/	1/1	6/1		7/	3/	1/	1/	16/1	2/	19/1	35/2
sp.			2/	4/	/2	6/2	5/		1/	6/	6/	22/	15/	43/	55/2
tuxeni**	Forsslund, 1957	P						1/		1/					1/
Neoliochthonius sp.nr. globuliferous				1/	4/	5/		1/		1/					6/
Sellnickochthonius circoides**	Weis-Fogh, 1948	P		29/6	1/1	3/7									30/7
immaculatus*	(Forsslund, 1942)	H	2/			2/	8/	1/	2/	11/	1/1		1/	2/1	15/
suecica*	Forsslund, 1942	H/A/S	6/	60/34	11/1	77/35		42		42		/1		/1	119/36
sp.nr. suecia								2/4		2/4					2/4
Synchthonius crenulatus*	(Jacot, 1938)	H						1/1		1/1					1/1
Verachthonius montanus*	(Hammer, 1952)	N/n					/1			/1					/1
sp.								13/		13/					13/
Pterochthoniidae															
Pterochthonius angelus*	(Berlese, 1910)	H	/1			/1	24/	4/	1/	29/					29/1
Mixonomata															
Euphthiracaridae															
Euphthiracarus cernuus**	Walker, 1965	N	3/		1/	4/	2/	3/	1/	6/					10/
sp.nr. monodactylus							/1			/1					/1
sp.nr. pluchellus					/1	/1									/1

Appendix B. continued.		Distribution	LOG LAKE fall	spring	summer	TOTAL	SKULOW LAKE fall	spring	summer	TOTAL	TOPLEY fall	spring	summer	TOTAL	OVERALL TOTAL
Oribotritiidae															
Protoribotritia															
sp.								2/		2/	1/	1/		2/	4/
Phthiracaridae															
Phthiracarus															
sp.1							1/1			1/1					1/1
bryobius**	Jacot, 1931	N					1/			1/					1/
Desmonomata															
Camisiidae															
Camisia															
lapponica*	(Trägårdh, 1910)	H										1/		1/	1/
spinifer*	(C.L.Koch, 1835)	H/O										1/1		1/1	1/1
Heminothrus															
longisetosus*	Willmann, 1925	H					1/		1/1	2/1	20/	25/1	29/	74/1	76/1
Neonothrus															
humicolus*	(Forsslund, 1955)	H									7/	3/2	5/3	15/5	15/5
Platynothrus															
nevadensis**	(Pérez-iñigo, 1969)	P	2/			2/									2/
peltifer	(C.L.Koch, 1893)	H/A		1/1		1/1					3/	1/1	3/	7/	8/2
septentrionalis**	(Sellnick, 1944)	P	1/		1/	2/	16/	3/		19/	/2			/2	21/2
sp.nr. septentrionalis							4/	2/	1/	7/					7/
Nothridae															
Nothrus															
anauniensis*	Canestrini et Fanzago, 1876	H/O/A							2/	2/					2/
borussicus*	Sellnick, 1929	H		1/		1/	15/	1/		16/					17/
palustris**	C.L.Koch, 1839	H						1/		1/					1/
sp.nr. monodactylus							1/			1/					1/
sp.nr. pluchellus															
Trhypochthoniidae															
Trhypochthonius															
tectorum	(Berlese, 1896)	H/n					1/		1/	2/			1/	1/	3/
Brachypylina															
Achipteriidae															
Anachipteria															
sp.2											1/			1/	1/
Dentachipteria															
sp.							1/			1/					1/
Ceratozetidae															
Ceratozetes															
cuspidatus*	Jacot, 1939	N	7/2	3/1	9/1	19/4	11/1	6/1	8/	25/2					44/6
thienemanni	Willmann,1943	H/n	4/5	6/3	4/2	14/10	5/	2/		7/	12/8	27/14	21/1	60/23	81/33
Dentizetes															
rudentiger*	Hammer, 1952	N					1/	1/	2/	4/					4/
Neogymnobates															
luteus*	(Hammer, 1955)	N						1/		1/	8/	6/	3/	17/	18/

			LOG LAKE				SKULOW LAKE				TOPLEY				OVERALL
		Distribution	fall	spring	summer	TOTAL	fall	spring	summer	TOTAL	fall	spring	summer	TOTAL	TOTAL
Appendix B. continued.															
Galumnidae															
Pilogalumna															
sp.nr. tenuiclava							5/	4/	1/	1/	4/	6/	3/1	13/1	23/1
sp.nr. ornatula							2/			2/	2/			2/	4/
Oribatulidae															
Jornadia															
n.sp.**							34/2	3/	9/2	46/4					46/4
Oribatula															
tibialis*	(Nicolet, 1855)	H	9/2	5/	2/	16/2			1/	1/	14/	16/4	4/	34/4	51/6
Phenopelopidae															
Eupelops															
sp.nr. plicatus*							1/1	2/		3/1					3/1
Scheloribatidae															
Scheloribates															
sp.1							22/28	33/16	/7	55/51			1/	1/	56/51
Mycobatidae															
Mycobates															
incurvatus*	Hammer, 1952	N					4/2	2/	4/1	10/3					10/3
punctatus*	Hammer, 1955	H	1/			1/	/2		/1	/3					1/3
Damaeidae															
Belba															
sp.											1/	7/	1/	9/	9/
Epidamaeus															
koyukon*	Behan-Pelletier and Norton, 1985	N						1/		1/			1/	1/	2/
sp.nr. coxalis*			2/	2/2	1/	5/2					7/	12/	11/	30/	35/2
sp.nr. floccosus*												1/		1/	1/
sp.nr. kodiakensis*									2/	2/	4/			4/	6/
Eremaeidae															
Eremaeus															
brevitarsus*	(Ewing, 1917)	N									3/	26/	12/2	41/2	41/2
translamellatus**	Hammer, 1952	H		3/	1/	4/	9/1	10/4		19/5	2/	2/	7/3	11/3	34/8
Eueremaeus															
chelous**	(Higgins) comb.nov.	N		1/		1/									1/
marshalli	Behan-Pelletier, 1993	N							1/	1/					1/
sp.nr. marshalli									1/	1/					1/
Gymnodamaeidae															
Gymnodamaeus															
sp.nr. laedaceus*			6/	7/	5/	2/		2/		2/					22/
Liacaridae															
Liacarus															
bidentatus	Ewing, 1918	N			1/	1/									1/
Metrioppidae															
Ceratoppia															
quadridentata arctica	Hammer, 1955	H							2/	2/					2/

		Distribution	LOG LAKE fall	spring	summer	TOTAL	SKULOW LAKE fall	spring	summer	TOTAL	TOPLEY fall	spring	summer	TOTAL	OVERALL TOTAL
Appendix B. continued.															
Oppiidae															
Moritzoppia clavigera*	(Hammer, 1952)	H									122/142	147/49	315/32	584/223	584/223
Multioppia sp.*							1/	21/	7/1	29/1	1/	6/		7/	36/1
Oppia sp.1*							12/	11/	4/	27/					27/
Oppiella nova	(Oudemans, 1902)	C	341/16	24/34	362/11	907/213	424/16	487/155	81/123	992/447	192/72	715/17	328/8	1235/97	3134/757
washburni*	(Hammer, 1952)	N	24/9			24/9						20/		20/	44/9
Quadroppia quadricarinata*	(Micheal, 1885)	C	/3	14/1	7/	21/	24/	8/	4/	36/	4/		11/	15/	72/4
Suctobelbidae															
Suctobelba sp.1*			2/			2/	1/			1/	1/	2/	3/	6/	9/
sp.2*			/1			/1			1/1	1/1			1/	1/	2/2
sp.3*											1/			1/	1/
Suctobelbella sp.nr. acutidens*			4/8	3/7	10/4	17/22	27/3	16/3	18/7	61/13	116/5	84/8	96/3	296/16	374/51
sp.nr. subcornigera*									2/	2/					2/
sp. 2			/2	6/	7/4	13/6	1/			1/	6/	15/	6/	27/	41/6
sp. 3			1/2	1/	/2	2/4	4/			4/	25/2	4/	1/	30/2	36/6
sp.4									/1	/1		4/2		4/2	4/3
sp.5											1/		2/	3/	3/
sp.6			4/6		5/	9/6		4/	2/1	6/1	27/1	17/	39/1	83/2	98/18
sp.7			/2	2/3	/1	2/6					2/	/1	/4	2/5	4/11
sp.8			5/1	/3		5/4						4/		4/	9/4
sp.9									1/	1/	3/			3/	4/
Tectocephidae															
Tectocepheus velatus	(Micheal, 1880)	C					41/3	24/1	7/	72/4	2/	3/	6/	11/	83/4
Cepheidae															
Cepheus corae *	(Jacot, 1928)	N					1/	1/		2/					2/
Undetermined sp.1				1/		1/									1/
Undetermined Juveniles			48/22	56/23	83/4	187/49	468/58	77/31	34/12	579/110	122/45	184/17	191/6	497/68	1263/218

* indicates new record for British Columbia
** indicates new record for Canada

Chapter 5. Short-term impact of soil compaction and organic matter removal on soil mesofauna density and oribatid mite diversity.

5.1 Introduction

Soil fauna are integral to humus formation (Klinka et al. 1981) and the release of important plant nutrients through mineralization of organic matter (Seastedt 1984, Setälä 1995). Thus, knowledge of the diversity and distribution of soil organisms as well as understanding of their role in soil processes might be applied to maintain high nutrient cycling and good plant growth within well-managed forest ecosystems (Marshall 1993). Furthermore, changes to faunal assemblages may be detected prior to changes in physical or chemical properties, thus making soil fauna useful indicators of site degradation processes (Garay and Nataf 1982).

Development of silvicultural practices that would satisfy forestry objectives and, at the same time, favourably influence soil fauna to enhance soil fertility (Marshall 1989) should be of primary importance. In 1991, the BC Ministry of Forests established the Long Term Soil Productivity Study (LTSPS) (Hope et al. 1991, Powers et al. 1990) in conjunction with a similar research program in the United States (see Powers 1989). This study addresses effects of various levels of soil compaction and organic matter removal on long-term soil productivity in the Sub-Boreal Spruce (SBS) biogeoclimatic zone over a full rotation period (80-120 years on SBS sites).

Silvicultural practices, such as forest harvesting and site preparation, modify a variety of physical, chemical and biological properties in the soil, consequently affecting soil pore space, composition and amount of organic matter, forest floor and mineral soil temperatures and soil moisture. Alteration of these properties, in turn, can adversely affect soil fauna density and diversity (Hill et al. 1975, Cancela da Fonseca 1990, Marshall 1993) as well as alter their living space and food supply (Shaw et al. 1991).

Two features of the soil ecosystem, organic matter and soil porosity, can be related to all alterable soil properties that influence soil productivity (Powers et al. 1990). Organic matter supplies nutrients in soil, influences soil structure (Banerjee and Sanyal 1991) and provides living space for more than 80% of soil fauna and flora in the forest soil ecosystem (Wallwork 1970, Price 1975). Thus, changes in the quality and quantity of organic matter input can directly influence biological activity. Soil porosity, determined by soil structure and texture, directly influences soil physical properties, such as aeration, water storage, infiltration and flow (Childs et al. 1989), which can be adversely affected by soil compaction. Soil compaction also reduces soil pore space which impedes the movement of soil fauna since most soil fauna do not actively burrow in the soil, but utilize existing channels and openings in the soil to move around (Wallwork 1970).

Numerous studies have explored, separately, the impact of harvesting practices and soil compaction on soil fauna communities. Harvesting methods such as clear cutting (Huhta et al. 1967, Huhta et al. 1969, Vlug and Borden

1973, Blair and Crossley 1988), whole tree and stem only harvesting (Bird and Chatarpaul 1986 and 1988) and selective logging (Hoekstra et al. 1995) reduce the density and change the structure of the soil fauna community. Likewise, soil compaction, caused by human trampling (Garay and Nataf 1982, Borcard and Matthey 1995), animal (Vtorov 1993) and mechanical activity (Smeltzer et al. 1986, Kevan et al. 1995), also reduces density and diversity of soil fauna. To date there has been no single study that has addressed the impact of both organic matter removal and soil compaction together on soil fauna.

The LTSPS experiment provided an excellent opportunity to examine the impact of organic matter removal and soil compaction on soil fauna. I report here on the short-term impact of soil compaction and organic matter removal on density and relative abundance of soil mesofauna and diversity of oribatid mite species and establish the basis for monitoring long-term recovery of the soil fauna community throughout a full rotation period.

5.2 Materials and Methods

5.2.1 Study site

This study was conducted within the Sub-Boreal Spruce (SBS) zone in the central interior of British Columbia (Figure 2.1). Refer to Chapter 2 for further information on site descriptions, plot layout and treatment application at the three replicate installations of the Long Term Soil Productivity Study.

5.2.2 Plot selection, layout and treatment application

Between 1991 and 1993, nine treatment plots (40 m x 70 m) were established at each site. Three 3.0 x 3.0 m plots were also located at each site in an unharvested area (>1 ha in size) set aside as a forest control (OM0C0) adjacent to the treatment plots (Figure 2.1). The LTSPS treatments were a factorial combination of each of three levels of soil compaction (none [C0], light [C1] and heavy [C2]) with each of three levels of organic matter removal (stem only [OM1], whole tree [OM2] and whole tree/forest floor [OM3]) (Hope et al. 1991, Holcomb 1996). Plots were harvested in winter after a compressed snow pack had been established. Treatment application continued on each site the first summer following harvest. An excavator removed slash from whole tree harvested plots as well as the forest floor on whole tree/forest floor removal plots. A compaction plate mounted on the arm of an excavator was used to compact the soils on each plot. A 2 cm deep depression was made for each light compaction treatment and a 4 cm deep depression was achieved on heavy compaction plots. For further information on treatment application, see Trowbridge et al. (1996).

5.2.3 Sampling, sorting and identification of soil fauna

Samples for soil mesofauna were collected from six plots at each installation, the uncut forest (control) (OM0C0) and five treatment combinations: 1) stem-only removed, no compaction (OM1C0); 2) whole tree/forest floor removed, no compaction (OM3C0); 3) whole tree removed, light compaction

(OM2C1); 4) stem-only removed, heavy compaction (OM1C2); 5) whole tree/forest floor removed, heavy compaction (OM3C2). Because of time and financial constraints, sampling was limited to the treatment extremes.

All plots at each site were sampled in the same phenological windows for two years (1994 at Topley and Log Lake; and 1995 at Skulow Lake). Timing of sample collection was based on: bud burst on trembling aspen (spring); soil temperature of 10 °C at 10 cm (summer) and leaf colour change in trembling aspen (fall). In addition to standardizing sampling times among sites, these indicators relate to biological activity in the soil and span the range of seasonal variation in distribution and life stages for soil fauna at these sites.

For each sampling date, one soil core (4.5 cm in diameter) was removed from each of three randomly selected subplots (2.5 m x 2.5 m in the treatment plots and 0.5 x 0.5 m in the control plots) in each of the six plots (downed logs or large rocks were avoided). The top 3 cm from both the organic and mineral soil horizons were sampled from each core. Only mineral soil samples could be collected from plots that had the forest floor removed (OM3). Each subplot was sampled only once during the study in order to limit the impact of soil removal.

Within 48 hours of collection, samples were placed in a high-gradient extractor for one week (Lussenhop 1971) with data loggers motoring the temperature gradient during the extraction process. Mesofauna were collected into a 0.6% (w/v) picric acid solution and then transferred into 1-dram glass shell vials with 70% ethanol by washing the contents of the collecting dishes with distilled water through a 50 µm sieve until no picric acid remained.

All samples were initially sorted and counted under a dissecting microscope. Collembola were identified to family, and Acari to suborder. Within the samples, several taxa, other than Acari and Collembola, occurred at very low densities. These were pooled into one group, hereafter referred to "Other mesofauna". All mesofauna samples are stored with the B.C. Ministry of Forests Research Branch Laboratory, P.O. Box 9536 Victoria, B.C. V8W 9C4

Oribatid specimens were sorted to morphospecies under a dissecting microscope, cleared with lactic acid, temporarily mounted on cavity slides and identified to species under a compound microscope (Norton 1990). Identifications were carried out using Balogh and Balogh (1992), Norton (1992), Norton (1990), Balogh and Mahunka (1983) as well as other published species keys and original species descriptions. Dr. Valerie Behan-Pelletier (Agriculture Canada Eastern Cereal and Oilseed Research Centre, Ottawa) checked species identifications. Classification of oribatid species follows Marshall et al. (1987). Numbers of individuals per taxon were recorded for each sample. Voucher specimens will be deposited with Biodiversity Assessment and Evaluation Research Branch, Agriculture Canada Eastern Cereal and Oilseed Research Centre, K.W. Neatby Building, Central Experimental Farm, Ottawa, Ontario K1A 0C6.

5.2.4 Data analyses

5.2.4.1 Mesofauna

Density (number of individuals per sample) and relative abundance ([number of individuals per taxon/total individuals collected in the sample] x 100) were used in analyses. Density is useful for estimating population size and determining changes in absolute abundance while relative abundance is useful to compare the structure of soil fauna assemblage and the structural similarity among sites, treatments or horizons (Wallwork 1976). Density (number of individuals/m^2) and relative abundance (% of total) are reported as mean ± standard error, unless stated otherwise.

Only taxa representing ≥1% of all collected material were considered for further analysis since analysis of these rare taxa had limited value. Data were transformed to meet assumptions of normality before analyses; density data were log transformed [$\log_{10}$ (X+1) where X = actual count of individuals for a taxon] and relative abundance data were arcsine transformed (arcsin$\sqrt{p}$ where p = relative abundance of the taxon). A non-parametric test of ranked scores was used for those taxa that did not have normally distributed data (SAS 1990).

Separate analyses were carried out on two data sets: 1) the organic horizon and mineral soil data combined (hereafter referred to as combined) and 2) the mineral soil data only. Since the sites are considered true replicates (Trowbridge et al. 1996), both data sets were analyzed to assess relative impacts of organic matter removal and soil compaction. A nested 2 X 2 ANOVA design [two levels of organic matter removal (stem-only and whole tree/forest floor) and two levels

of soil compaction (none and heavy) with treatment combinations nested by site] was used. Values for the uncut forest control and whole tree/light compaction plots are also presented for comparison. These plots were not included in the analyses because they cannot be included in the factorial design (i.e. no compaction in the control area and only one OM2 plot sampled).

Statistical significance was judged using the Type III sums of squares for both ANOVA procedures. Test statistics (F or χ^2 values) and probabilities are presented when differences are significant. All statistical tests used in this study were conducted using the SAS General Linear Models (GLM) procedure (SAS 1990) with $\alpha = 0.05$.

5.2.4.2 Oribatid mites

Three diversity indices including the exponential form of Shannon-Wiener Index (N_1) (Hill 1973), the reciprocal of Simpson's Index (N_2) (Hill 1973), and the modified Hill's ratio for evenness (E) (Ludwig and Reynolds 1988), as well as the average number of species/sample were determined for each sample (see Appendix A for equations). Comparison of these diversity values among treatments followed the same procedure as for the density and relative abundance of the soil mesofauna (see Section 5.2.4.1 above).

Relative abundance of each oribatid mite species was plotted to examine the impact of organic matter removal and soil compaction on the species assemblage. Hågvar (1994) proposed that a lognormal distribution of relative abundance values for species was typical for non-stressed soil microarthropod

populations. In stressed or disturbed environments, the relative abundance of some species will decrease while the relative abundance of a few species will increase which skews the distribution of relative abundance values from lognormal (Hågvar 1994).

Species accumulation curves for oribatid mite assemblages were estimated using rarefaction. Rarefaction compensates for differences in sampling effort (in this case the number of individuals collected) and estimates the number of species expected in a random sample of individuals drawn from a collection (Krebs 1989).

5.3 Results

5.3.1 Total soil mesofauna

Densities of total soil mesofauna in both the combined (Figure 5.1) and mineral soil (Figure 5.2) data were significantly lower on plots with whole tree and forest floor removal (OM3) than on plots with stem only removal (OM1) ($F_{3,107}$=72.23, $p<0.0005$ and $F_{3,107}$=8.97, $p<0.0001$, respectively). Density of total soil mesofauna also differed significantly between no (C0) and heavy (C2) soil compaction in both combined and mineral soil data ($F_{3,107}$=15.38, $p<0.0005$ and $F_{3,107}$=3.48, $p=0.019$, respectively). However, density of total soil mesofauna was higher in plots that retained the forest floor, even with heavy soil compaction (OM1C2), than in plots where the forest floor had been removed (OM3)

Figure 5.1. Comparison of mean density of total mesofauna (±SE) from combined organic and mineral data among treatments (sites and seasons pooled).

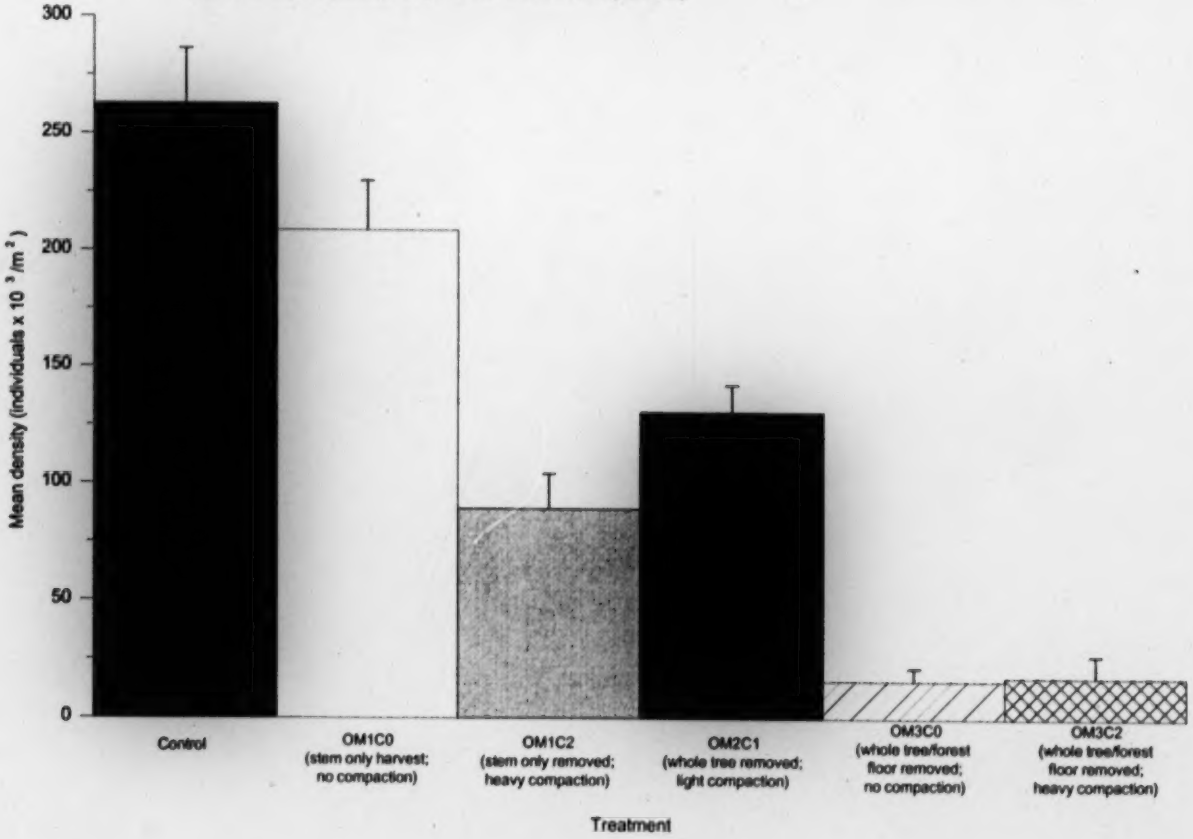
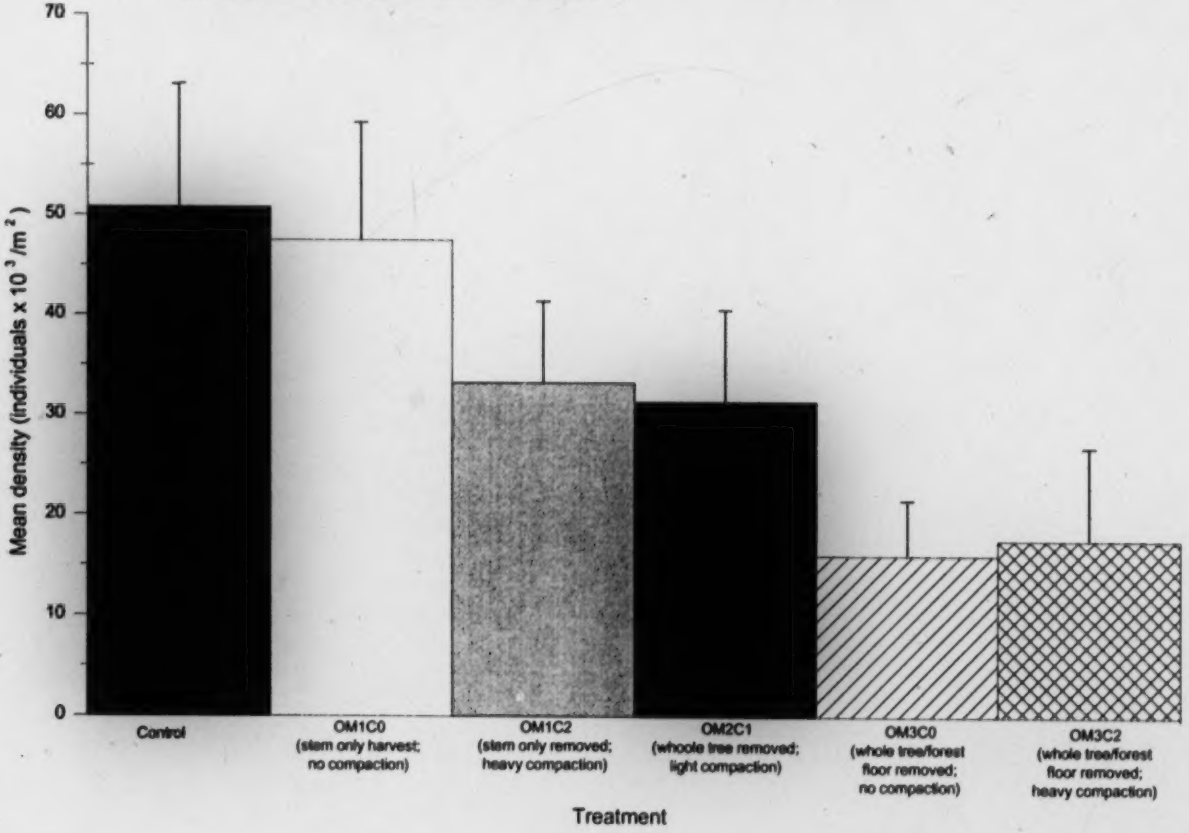


Figure 5.2. Comparison of mean density of total mesofauna (±SE) from the mineral soil among treatments (sites and seasons pooled).



regardless of the level of soil compaction (Figures 5.1 and 5.2). Loss of forest floor in the OM3 plots is significant since most soil fauna reside here. Stem-only harvested plots included fauna from both the organic horizon and mineral soil whereas OM3 plots included only fauna from the mineral soil.

Density of total soil mesofauna in stem-only harvested plots was similar to densities in the uncut forest control plots for both combined and mineral soil data and substantially higher than the other three treatments (stem-only harvesting combined with heavy soil compaction; whole-tree/forest floor removal alone and whole tree/forest floor removal with heavy soil compaction). Organic matter removal had a greater influence on densities than soil compaction, accounting for almost 60% of the variation in mesofauna density. Densities of the remaining mesofauna taxa examined in the combined and mineral soil followed a similar pattern (Tables 5.1 and 5.2, respectively).

Relative abundances of Hypogastruridae ($F_{3,107}$=6.54, $p<0.0005$), Onychiuridae ($F_{3,107}$=9.14, $p<0.0005$), Isotomidae ($F_{3,107}$=10.54, $p<0.0005$) and Oribatida ($F_{3,107}$=5.96, $p<0.0005$) were significantly lower in the whole tree/forest floor harvested plots than the stem-only harvested plots in the combined data (Figure 5.3). Conversely, the relative abundance of Prostigmata was significantly higher in the whole tree/forest floor harvested plots than the stem only harvested plots ($F_{3,107}$=2.91, $p<0.05$). In the mineral soil, relative abundances of Onychiuridae ($F_{3,107}$=8.70, $p<0.0005$), Isotomidae ($F_{3,107}$=6.04, $p<0.005$) and Oribatida ($F_{3,107}$=3.44, $p<0.0005$) were significantly lower in the whole tree/forest floor harvested plots than the stem only harvested plots (Figure 5.4).

Table 5.1. Comparison of mean density ($x\ 10^3/m^2$) ± SE of soil mesofauna from the combined organic horizon and mineral soil data among four treatments. (OM1=stem-only harvest; OM2=whole tree; OM3=whole tree/forest floor removal; C0=no compaction; C1=light compaction; C2=heavy compaction)

		TREATMENTS					STATISTICAL RESULTS		
	Control	OM1C0	OM1C2	OM2C1	OM3C0	OM3C2	Method	OM1 vs. OM3	C0 vs C2
Hypogastruidae	4.0 ±0.95	3.3 ±0.77	2.2 ±0.78	1.7 ±0.53	0.1 ±0.04	0.3 ±0.22	np*	22.26***	4.45*
Isotomidae	21.5 ±3.08	21.9 ±3.39	20.3 ±7.59	18.8 ±3.37	2.4 ±1.07	1.2 ±0.78	A**	42.84***	10.0***
Onychiuridae	16.7 ±4.66	17.2 ±3.60	2.7 ±0.81	6.9 ±1.87	1.0 ±0.40	0.3 ±0.19	np	33.01***	15.57***
Total Collembola	45.4 ±6.44	43.7 ±6.18	25.4 ±7.98	28.2 ±4.64	3.5 ±1.42	2.0 ±1.28	A	54.66***	17.38***
Oribatida	77.3 ± 11.61	57.4 ± 10.04	22.2 ± 5.09	34.7 ±4.28	4.0 ±1.50	3.1 ±2.71	A	85.95***	23.45***
Mesostigmata	11.0 ±1.19	9.0 ±1.11	4.1 ±1.18	5.2 ±1.06	0.6 ±0.27	1.7 ±1.13	A	43.19***	11.45***
Prostigmata	118.5 ±12.78	92.7 ±11.73	33.3 ±4.38	57.5 ±8.39	7.3 ±2.67	10.0 ±4.52	np	38.23***	18.25***
Total Acari	209.0 ±19.60	159.5 ±18.03	59.7 ±8.60	97.7 ±9.92	11.9 ±4.32	14.8 ±7.80	A	64.66***	13.65***

*np indicates analysis carried out using non-parametric test on ranked scores, $\chi^2_{3,107}$ value reported.
**A indicates analysis carried out using ANOVA procedure, $F_{3,107}$ value reported
* $p<0.05$, *** $p<0.0005$

Table 5.2. Comparison of mean density (x $10^3/m^2$) ± SE of soil mesofauna from the mineral soil among four treatments.
(OM1=stem-only harvest; OM2=whole tree harvest; OM3=whole tree/forest floor removal; C0=no compaction; C1=light compaction; C2=heavy compaction)

		TREATMENTS					STATISTICAL RESULTS		
	Control	OM1C0	OM1C2	OM2C1	OM3C0	OM3C2	Method	OM1 vs. OM3	C0 vs C2
Hypogastruidae	0.8 ±0.58	0.9 ±0.40	0.4 ±0.27	0.1 ±0.10	0.1 ±0.04	0.3 ±0.22	np[+]	ns[$]	ns
Isotomidae	2.0 ±0.50	4.7 ±1.47	5.3 ±1.85	2.5 ±0.77	2.4 ±1.07	1.2 ±0.78	A[**]	4.75**	ns
Onychiuridae	3.0 ±0.86	4.5 ±1.78	1.1 ±0.36	1.1 ±0.38	1.0 ±0.40	0.3 ±0.19	np	11.85***	5.23**
Total Collembola	5.9 ±1.39	10.4 ±3.54	6.8 ±2.16	4.0 ±0.87	3.5 ±1.42	2.0 ±1.28	A	8.07***	ns
Oribatida	15.6 ±4.84	16.2 ±5.97	5.9 ±2.42	5.2 ±1.68	4.0 ±1.50	3.1 ±2.71	A	8.50***	6.48***
Mesostigmata	1.6 ±0.45	1.8 ±0.47	1.1 ±0.57	0.9 ±0.49	0.6 ±0.27	1.7 ±1.13	A	3.94*	3.53*
Prostigmata	23.9 ±7.76	16.9 ±4.96	15.6 ±4.25	19.7 ±8.42	7.3 ±2.67	10.0 ±4.52	A	3.84*	ns
Total Acari	43.1 ±11.58	34.9 ±9.56	23.2 ±6.02	26.1 ±8.96	11.9 ±4.32	14.8 ±7.80	A	5.72**	3.26*

[+]np indicates analysis carried out using non-parametric test on ranked scores, $\chi^2_{3,107}$ value reported.
[**]A indicates analysis carried out using ANOVA procedure, $F_{3,107}$ value reported
$ ns indicates not significant
* p<0.05, **p<0.005, ***p<0.0005

Figure 5.3. Comparison of mean relative abundance (% of total) of soil mesofauna among treatments for organic and mineral data combined.

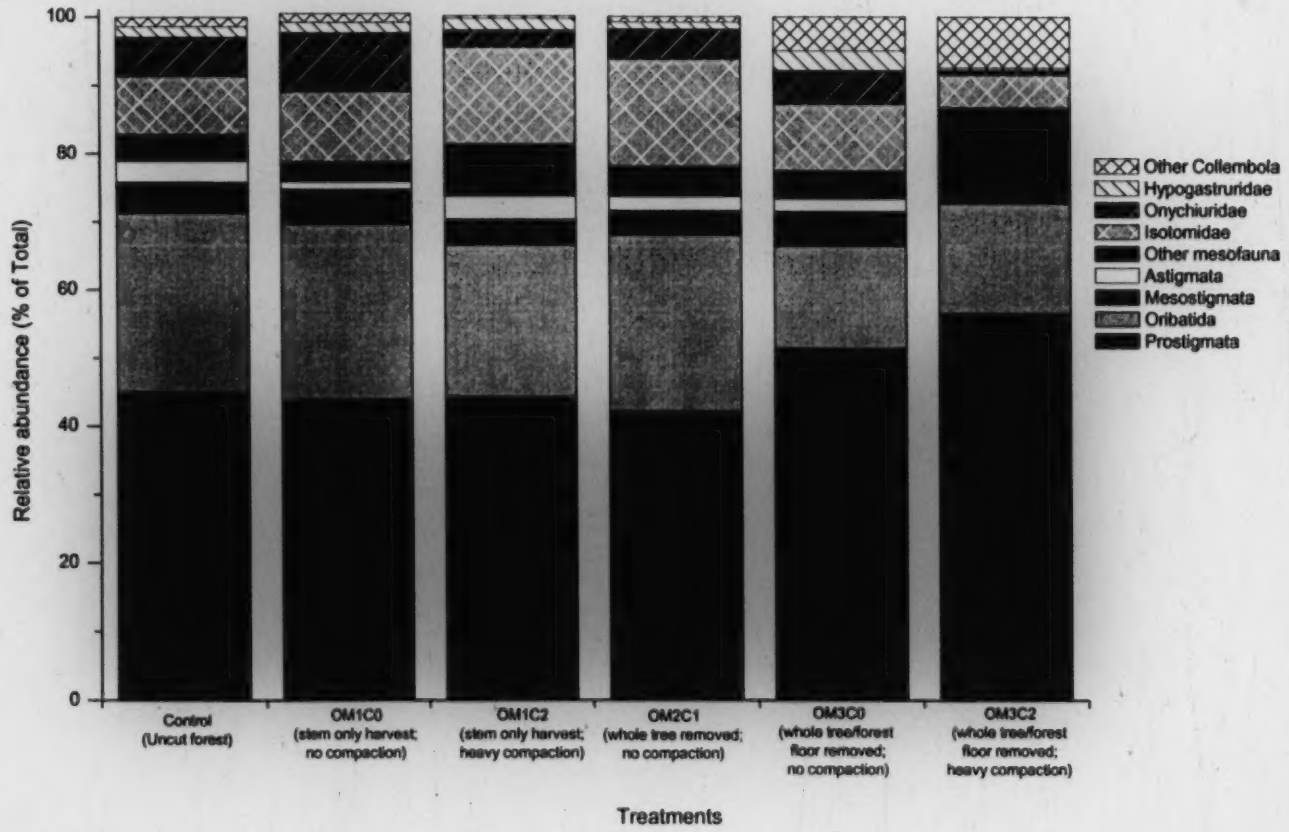
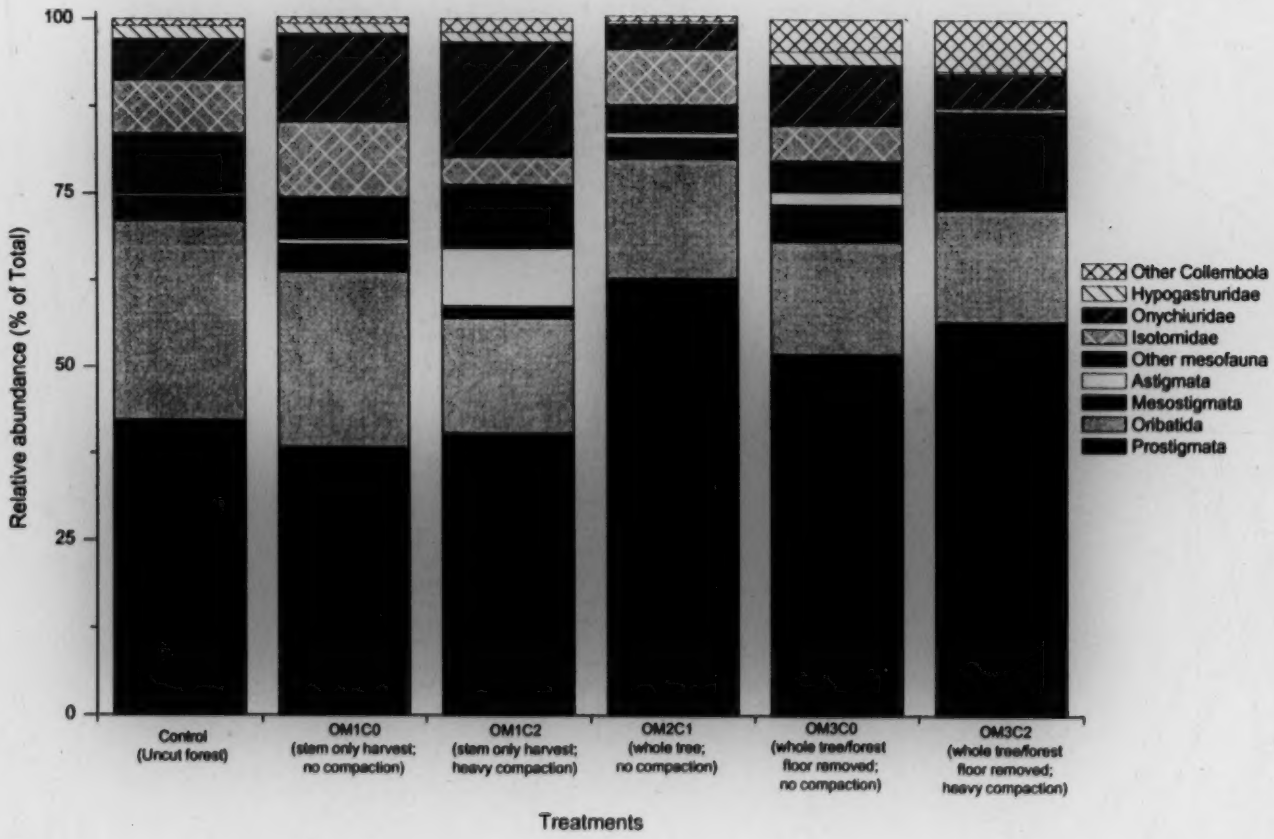


Figure 5.4. Comparison of mean relative abundance (% of total) of soil mesofauna collected in the mineral soil among treatments.



Onychiuridae was the only taxon influenced by soil compaction in both the combined and mineral soil data. Relative abundance of this family, composed of true soil dwelling species, was significantly lower in heavily compacted plots than in plots with no compaction for the combined soil data ($F_{3,107}$=8.98, p<0.0005) (Figure 5.3). In the mineral soil, the relative abundance of Onychiuridae was also significantly reduced under heavy compaction ($F_{3,107}$=6.46, p<0.0005) (Figure 5.4). However, even here, relative abundance was higher in stem only/ heavy compaction plots than in whole tree-forest floor removal/ no compaction plots. Again, the forest floor remaining on the stem only plots seems to have reduced the impact of soil compaction. Although the density of all taxa examined decreased, the shift in relative abundance indicated that Hypogastruridae, Onychiuridae, Isotomidae and Oribatida responded more negatively to disturbance than Prostigmata, which increased in overall relative abundance as treatment severity increased.

Overall, Acari was the dominant taxon in each of the treatment plots, representing 65-78% of the total mesofauna while Collembola accounted for 18-23 %. Prostigmata was the most abundant acarine suborder, representing approximately 39-46% of the mesofauna, followed by Oribatida (25-31%) and Mesostigmata (3-7%). Isotomidae, Onychiuridae and Hypogastruridae were the most abundant collembolan families. This pattern of relative abundance is similar to that observed in the uncut forest control (see Chapter 4).

5.3.2 Oribatid mites

Eighty-seven species of oribatid mites belonging to 49 genera and 28 families were identified (see Appendix B). Average number of species/sample was significantly lower in whole tree/forest floor removed plots than stem-only harvested plots ($F_{3,107}$=75.73, $p<0.0005$) (Figure 5.5a). Average number of species/sample was also significantly lower on plots with heavy compaction than on plots with no compaction ($F_{3,107}$=4.14, $p<0.05$) (Figure 5.5a).

As in the overall faunal analysis, changes to the diversity of oribatid mite species were influenced more by organic matter removal than soil compaction (Figure 5.5). Values of N_2, N_1 and evenness (E) (Figures 5.5 b, c and d, respectively) were significantly higher in stem only harvested plots than whole tree/forest floor removal (OM3) plots ($F_{3,107}$=18.63, $p<0.0005$, $F_{3,107}$=56.94, $p<0.0005$ and $F_{3,107}$=9.73, $p<0.0005$, respectively). Soil compaction did not alter N_2, N_1 or evenness significantly.

The combination of organic matter removal and heavy soil compaction influenced all aspects of diversity in the mineral soil except evenness (Figures 5.6 a-d). Diversity values (N_0, N_2, and N_1) (Figures 5.6 a, b and c, respectively) from the stem-only harvested plot (OM1C0) were similar to those values from the uncut forest control plot, indicating that stem only harvesting with no compaction had little impact on diversity in the mineral soil at these sites. Number of species (N_0), N_2 and N_1 from both stem only harvested/heavy compaction (OM1C2) plots and whole tree-forest floor removal/no compaction (OM3C0) plots were roughly equal. Diversity values on plots subjected to a combination of whole tree/forest

Figure 5.5 Comparison of mean diversity indices (±SE) among treatments for oribatid mite species from combined data. (OM1=stem only harvest; OM2=whole tree harvest; OM3=Whole tree/forest floor removed; C0=no compaction; C1=light compaction; C2=heavy compaction)

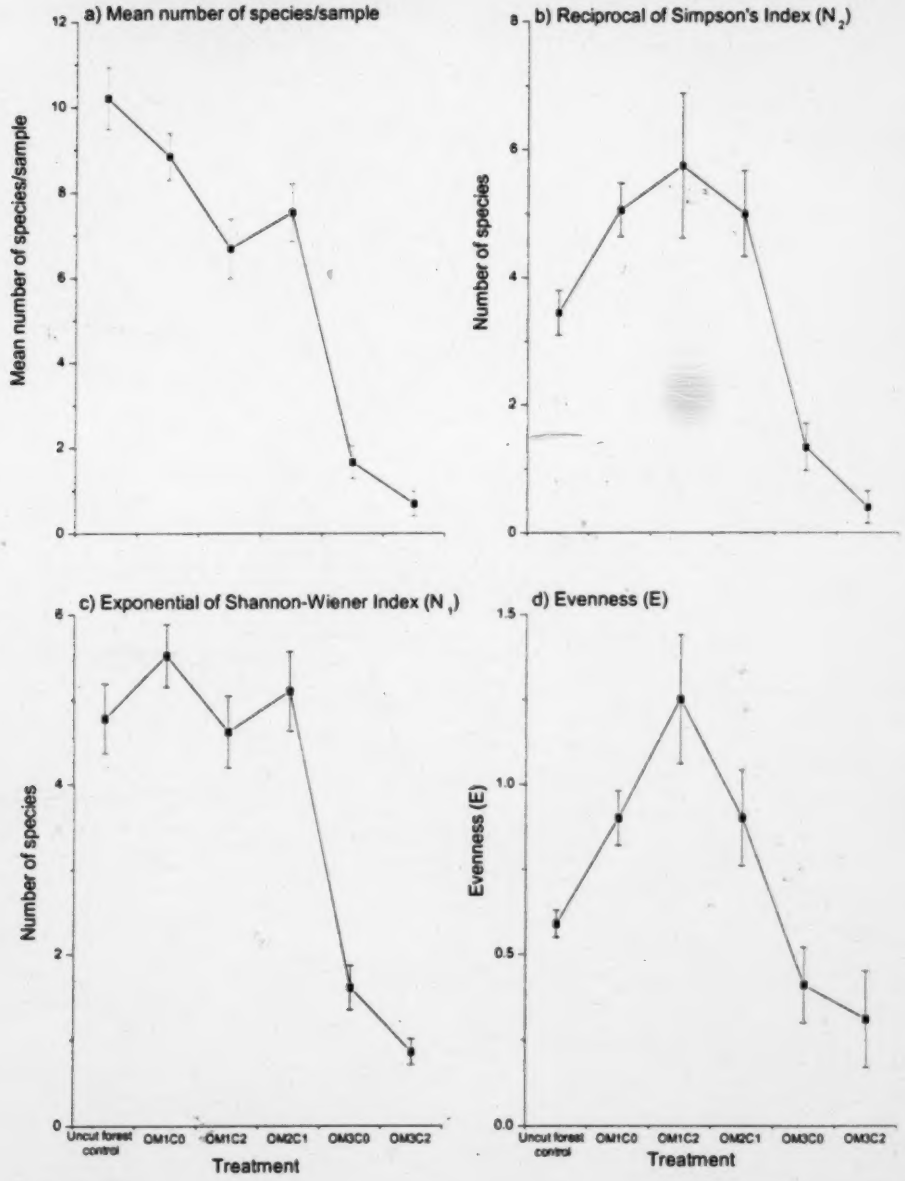
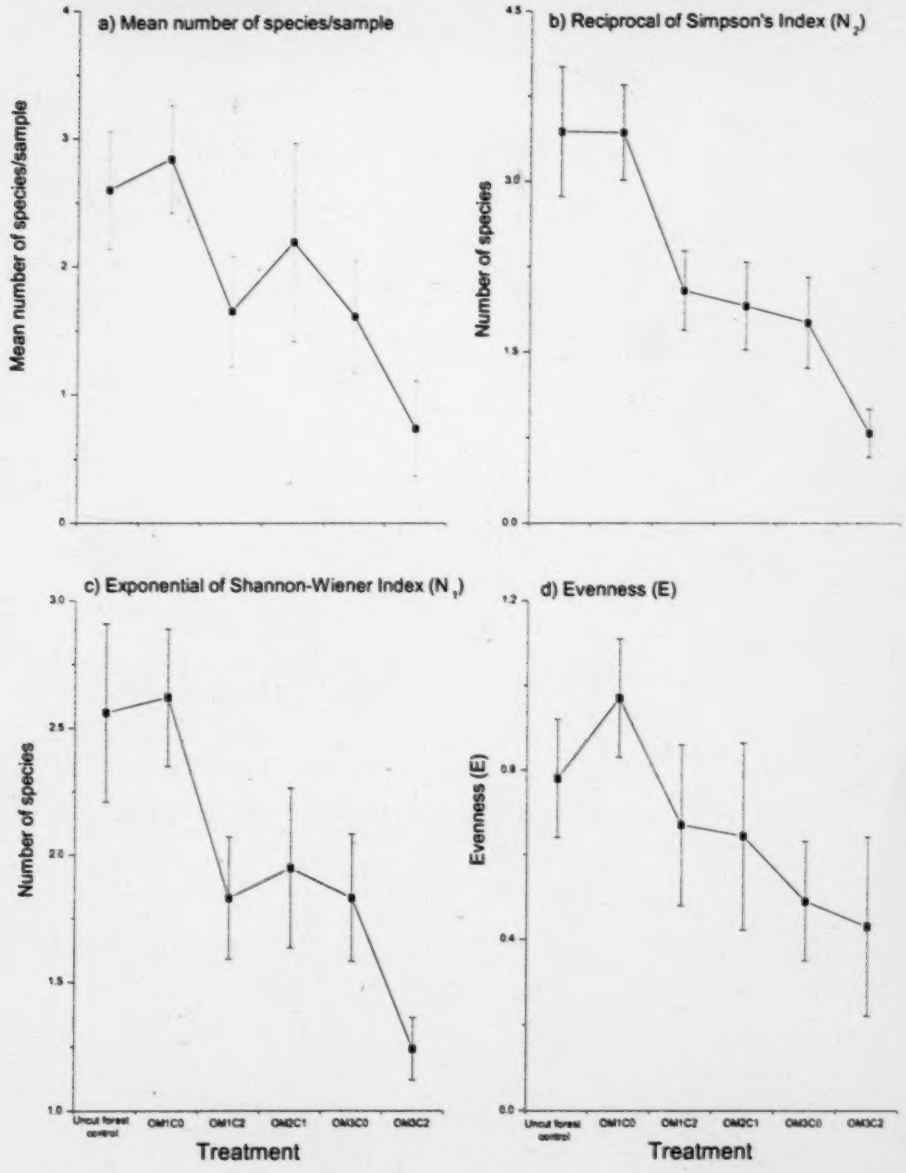


Figure 5.6 Comparison of mean diversity indices (±SE) among treatments for oribatid mite species from mineral soil data. (OM1=stem only harvest; OM2=whole tree harvest; OM3=Whole tree/forest floor removed; C0=no compaction; C1=light compaction; C2=heavy compaction)



floor removal and heavy soil compaction (OM3C2) were even lower than when each treatment was applied alone (i.e. stem only harvested/heavy compaction or whole tree-forest floor removal/no compaction).

There was a significant interaction between organic matter removal and soil compaction for evenness (E) in the mineral soil ($F_{5,107}$=4.14, $p<0.05$) (see Figure 5.6d). With the loss of rare oribatid species and increased dominance of Oppiella nova, evenness gradually decreased as treatment severity increased. A substantial loss of rare oribatid mite species (those representing <1% of the total collected) changed the structure of the oribatid mite species assemblage (Figures 5.7 and 5.8). For the combined data, 55 of 70 species (79%) collected in the uncut forest control were rare (Figure 5.7a). Percentage of rare species decreased to 42% in the OM3C2 plot (Figure 5.7f) and to 0% in the OM3C0 plot (Figure 5.7e), while the proportion of species with a relative abundance >1% increased from 19% in the uncut forest control to 100% in plots with whole tree/forest floor removed and no compaction. In the mineral soil of the uncut forest control, 23 of 33 species (70%) were rare (Figure 5.8a). After stem-only harvest, the proportion of rare species decreased to 40% (Figure 5.8b) and 0% in both whole tree/light compaction and whole tree-forest floor/no compaction plots (Figures 5.8d and e, respectively).

While the number of rare species decreased, identity of the abundant species remained, for the most part, consistent among treatment plots and these abundant species represented an increasingly greater proportion of the oribatid assemblage. In the combined data (Figures 5.7a-f), Oppiella nova was the

Figure 5.7. Comparison of log dominance of oribatid mite species from the organic and mineral soil combined among the treatments (all sites and seasons pooled). Black bars indicate those plots used in statistical analysis. The following names have been abbeviated: Oppiella nova , Suctobelbella sp.nr. acutidens

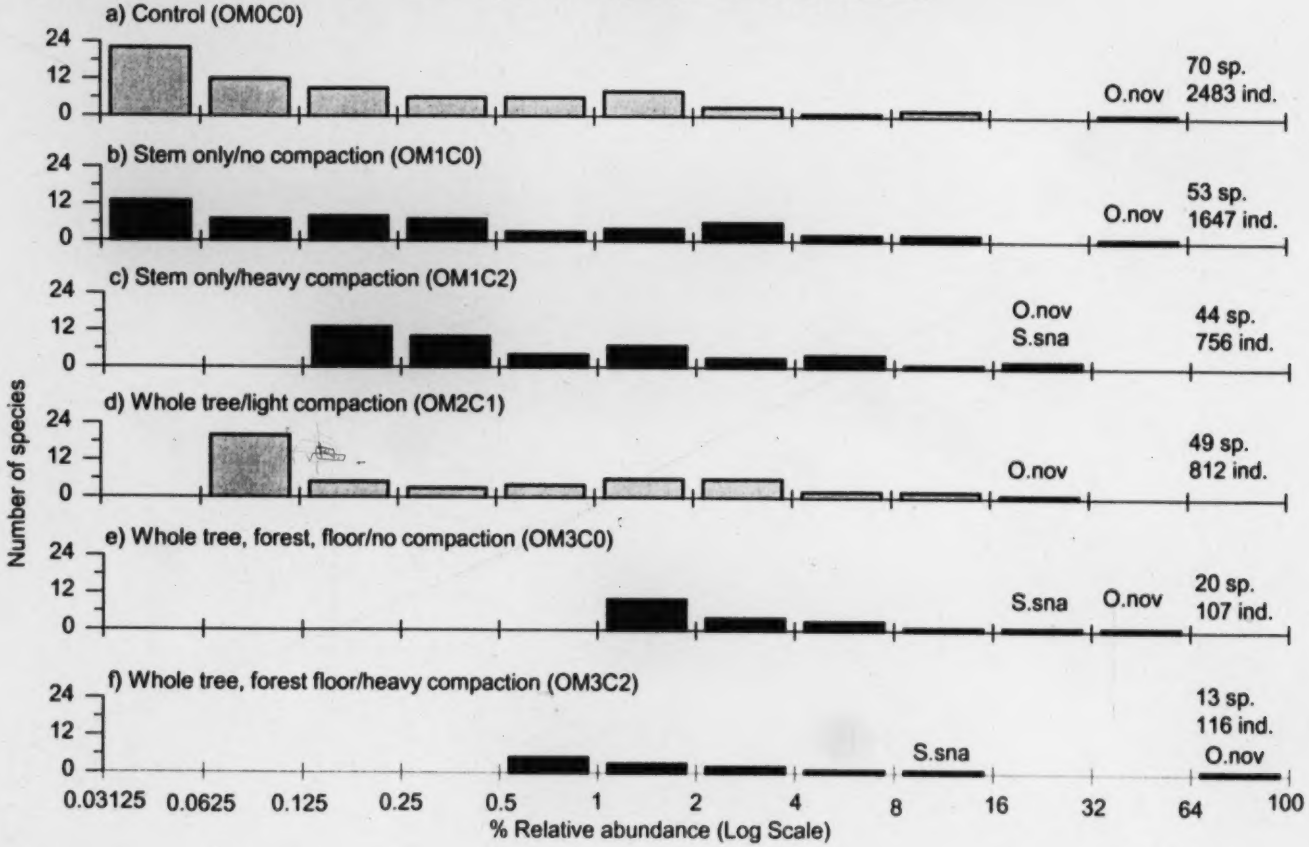
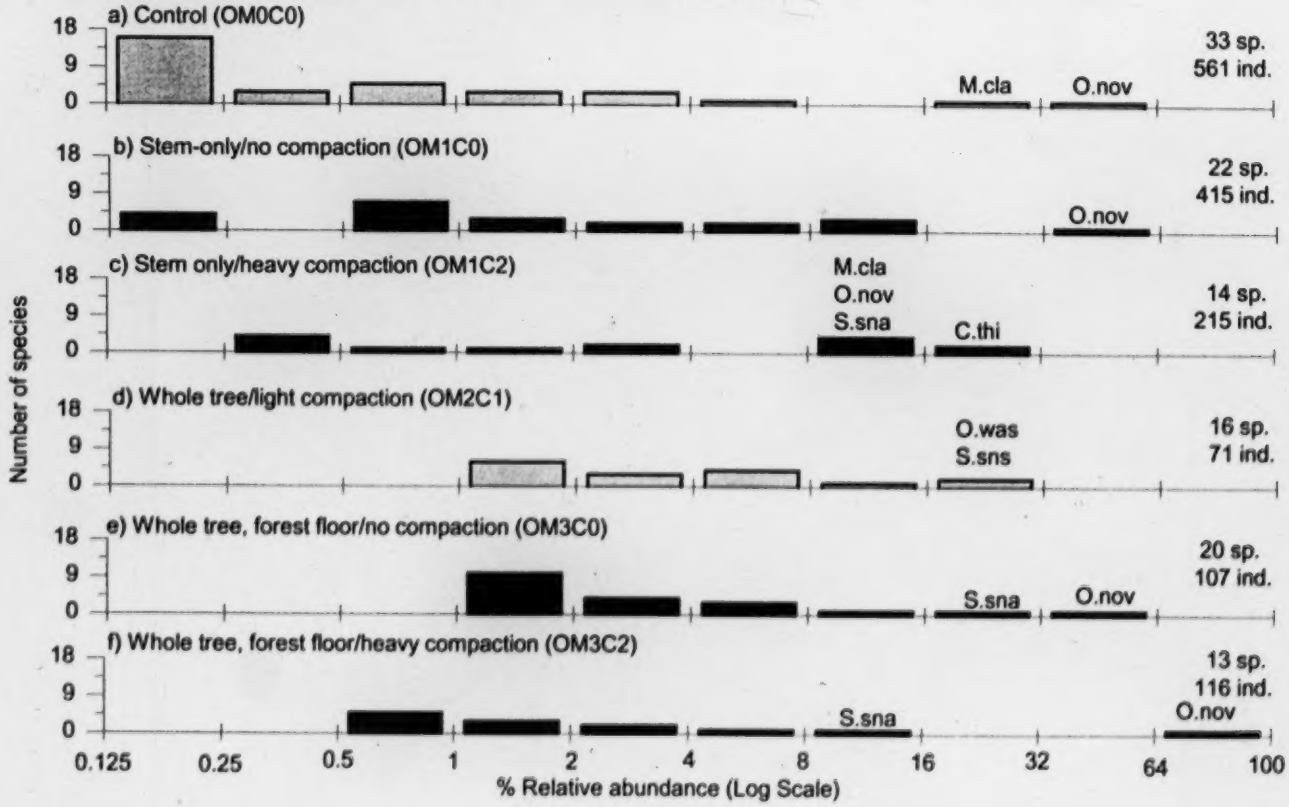


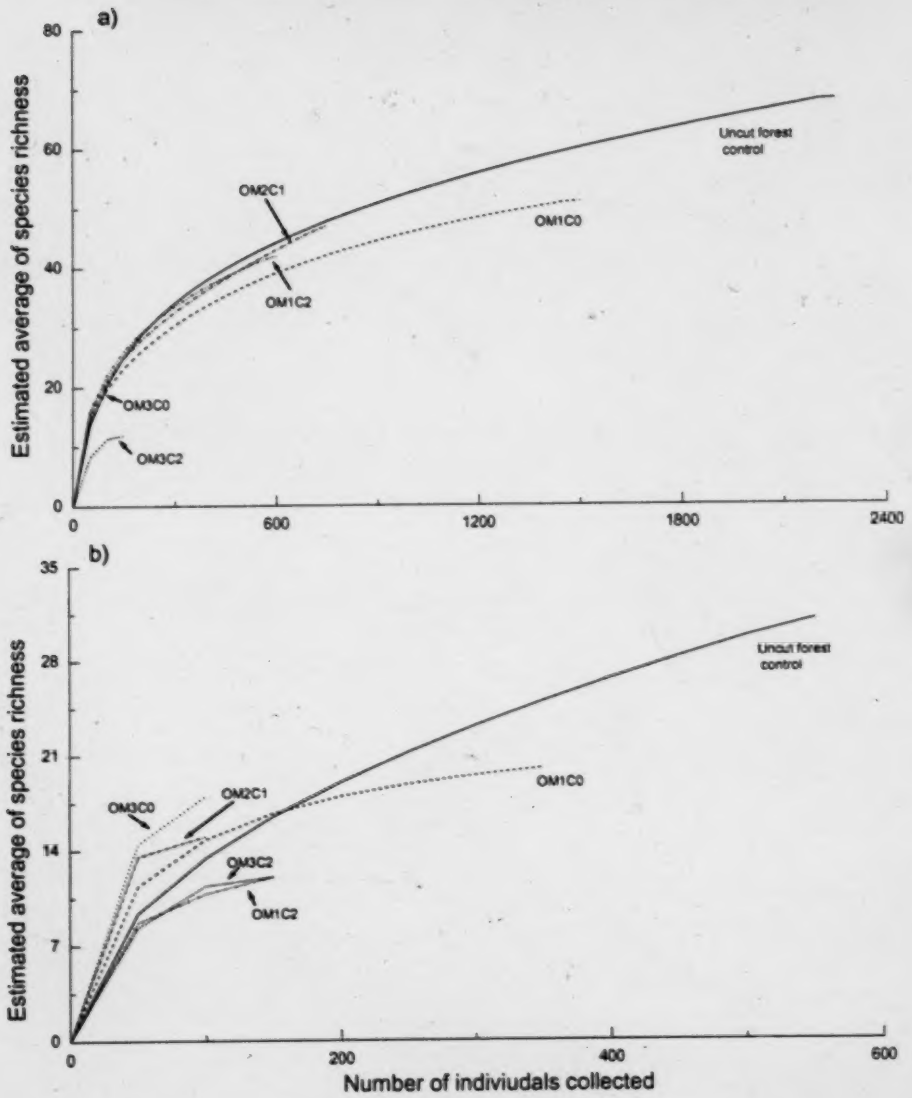
Figure 5.8. Comparison of log dominance of oribatid mite species collected in the mineral soil among treatments (all sites and seasons pooled). Black bars indicate those plots used in statistical analysis. The following names have been abbreviated: Oppiella nova , O. washburni , Suctobelbella sp.nr. acutidens , S. sp.nr. subcornigera, Moritzoppia clavigera, Ceratozetes thienmanni .



dominant oribatid species in all plots followed by Suctobelbella sp.nr. acutidens. In the mineral soil (Figure 5.8), O. nova was also the dominant species except in stem-only/heavy compaction plots (Figure 5.8c), which were dominated by Ceratozetes thiemanni, and whole tree/light compaction plots (Figure 5.8d) where Oppiella washburni was most common. Moritzoppia clavigera or S. sp.nr. acutidens were the second most abundant species in the mineral soil of the various treatment plots.

By controlling for differences in overall sample size, rarefaction analysis of the oribatid mite species assemblage supports the conclusion that species have been lost. In the combined data (Figure 5.9a), species accumulation in whole tree-forest floor/heavy compaction plots was much lower than the other plots. The remaining plots were characterized by similar species accumulation curves. However, species number on all treatment plots remained lower than the uncut forest control. In the mineral soil (Figure 5.9b), plots with heavy soil compaction had a lower rate of species accumulation than other treatment plots and the uncut forest control. The estimated number of species begins to level off between 75-100 individuals in all treatment plots except in whole tree-forest floor/no compaction, which has a rate of species accumulation that appears higher than the uncut forest control plot. This suggests lower species richness on treatment plots with compaction compared to the species richness in plots without compaction.

Figure 5.9. Rarefaction diversity analysis of oribatid mite species for the (a) combined [organic and mineral] and (b) mineral soil data of each treatment. OM1= stem only harvest; OM2=whole tree harvest; OM3=whole tree/forest floor removal; C0=no compaction; C1=light compaction; C3=heavy compaction.



5.4 Discussion

Soil mesofauna can respond to habitat disturbance in different ways. Huhta et al. (1967) documented three different responses of soil fauna communities to clearcutting in Norway spruce forests in Finland: i) a density increase immediately after cutting; ii) a density increase followed by a decrease several years after cutting; and iii) a density decrease immediately after cutting. In the present study, I found that stem-only harvesting without soil compaction did not significantly decrease the density of soil mesofauna immediately after timber harvesting compared to the uncut forest control. In fact, overall densities of two collembolan families, Isotomidae and Onychiuridae, were slightly higher in stem-only harvested plots than in uncut forest control plots. In the mineral soil alone, densities of Isotomidae and Onychiuridae as well as total Collembola, Oribatida and Mesostigmata in stem-only harvested plots did not differ significantly from those in the uncut forest control plots.

My results differ slightly from other studies. For example, two years after timber harvest in a temperate mixed conifer-hardwood stand, both conventional (stem-only) and whole-tree harvesting reduced microarthropod communities 56% to 68% (Bird and Chatarpaul 1986). In a Finnish study, densities of both collembolans and enchytraeids were higher in cut stands of Norway spruce than in uncut control stands immediately after timber harvesting, but mite (Acari) densities in cut stands were about half that of the control area (Huhta et al. 1967, 1969). I found that stem-only harvesting combined with heavy soil compaction

(OM1C2) decreased densities of most soil mesofauna taxa by 50% or more relative to the uncut forest control, which was similar to reductions observed by Bird and Chatarpaul (1986) and Huhta et al. (1967, 1969).

Generally, fungi dominate most forest soils and bacteria are prominent in agricultural soils (Wallwork 1970), thus most mites and springtails in forest soils feed on fungal biomass. However, tree harvesting and soil compaction can increase bacterial diversity and biomass in forest soils (Marshall 1998), thereby altering food resources (i.e. fungi) available to soil mesofauna. Declines in oribatid diversity and density have been related to the loss or delayed development of fungi in organic matter (Huhta et al. 1967). An increase in bacterial biomass could increase the density of microbial feeding species, such as members of the oribatid mite family Suctobelbidae (Ryabinin and Pan'kov 1987), altering the overall structure of a mesofaunal assemblage.

Loss of organic matter can also increase fluctuations in soil temperatures, light exposure at the soil surface and evaporation rates (Huhta et al. 1967, Shaw et al. 1991). Heat sum values (the sum of the daily average temperatures), calculated for six of the nine treatment plots at each site from September 20, 1996 to September 20, 1997, were higher on plots with greater compaction and more organic matter removal (Kranabetter and Chapman 1999). Although there were no extreme differences in soil temperature among treatments, temperature fluctuation increased with treatment severity, with soil temperatures going below freezing in winter and above air temperature in summer (M. Kranabetter, pers. comm.). Although most soil mesofauna taxa are able to tolerate a certain

degree of variation in soil temperature and moisture, some are unable to adapt to large fluctuations in these soil properties. For example, Siepel (1996) documented a decrease in densities of oribatid species intolerant to drought after forest harvesting.

Some oribatid species avoid drought conditions by moving deeper into the soil profile (Wallwork 1970, Siepel 1996). However, increased soil bulk density due to soil compaction can limit vertical movement in the soil profile, even for smaller species such as O. nova. In the present study, bulk density of the mineral soil was significantly higher in the heavy compaction plots than those plots with no compaction (see Chapter 2, Kranabetter and Chapman 1999). I found densities of mites and springtails were, in some cases, an order of magnitude lower in the heavy compaction plots compared to those plots with no compaction. Plots in which mineral soil was still covered by forest floor had higher densities of soil mesofauna than those plots where forest floor had been removed. The forest floor may act as a buffer, reducing the impact of compaction in the mineral soil and limiting the increase in bulk density. Donnelly and Shane (1986) showed that mulch applied prior to compaction reduced the degree of compaction.

Other soil compaction studies have shown reductions in the density of soil fauna. The abundance of total fungi, bacteria, nematodes and arthropods in a mixed northern hardwood forest in northwestern Vermont was reduced for up to two years after compaction (Smeltzer et al. 1986). Vehicle tracks significantly reduced densities of soil arthropods in the high Arctic tundra (Kevan et al. 1995).

Even walking can reduce the diversity and density of soil fauna. In deciduous forest soils near Paris, France, for example, soil compaction from human trampling reduced density and diversity of several mesofaunal groups, including Oribatida (especially Brachychthoniidae), by more than 50% (Garay and Nataf 1982). In Sphagnum mosses, human trampling dramatically reduced the number of oribatid mite species (Borcard and Matthey 1995). Compaction by grazing cattle in European pastures also reduced oribatid density and species diversity (Siepel, 1996).

Recovery of the soil fauna community may occur more rapidly in compacted soils than on sites with varying levels of organic matter removal. Bird and Chatarpaul (1986) suggested than faunal densities take 10-13 years to return to pre-harvest levels. For example, in a mixed hardwood stand in southwestern North Carolina, differences in mean density and relative abundance of microarthropod groups were still apparent between clear-cut and uncut sites eight years after harvest (Blair and Crossley 1988). However, in a mixed northern hardwood forest in northern Vermont, there were no detectable differences in fungal, bacterial, nematode or arthropod populations five years after soil compaction (Smeltzer et al. 1986). The impact of compaction on earthworms was of shorter duration than that of harvesting (Jordan et al. 1999). Furthermore, the elimination of compaction by feral pigs in Hawaiian rain forests nearly doubled soil microarthropod densities and increased the biomass of soil microarthropods by two and half times over seven years (Vtorov 1993).

As density and diversity of soil mesofauna decreased in the present study, structure of the mesofaunal assemblage also changed. For example, both density and relative abundance of oribatid mites declined significantly as treatment severity increased. While densities of Mesostigmata and Prostigmata also decreased, relative abundance of both taxa increased as treatment severity increased. Oribatid mites were more sensitive to changes in their environment and decreased in number at a greater rate than Prostigmata or Mesostigmata. Because of their rapid decline in both density and diversity in disturbed habitats, oribatid mites may be useful biological indicators (Behan-Pelletier 1999).

In the present study, I found that tree harvesting and forest floor removal reduced oribatid mite diversity and species richness and changed the structure of the oribatid mite species assemblage. Bird and Chatarpaul (1986) also found that relative abundance of several oribatid taxa differed significantly after harvesting but observed no change in the taxa present. In contrast, Siepel (1996) concluded that forest harvesting (a low frequency disturbance) reduced the number of oribatid species more than did natural disturbances, such as cyclical wildfires, or seasonal changes. He argued that species could accommodate natural disturbances through the development of life-history tactics or specific physiology.

More than 70% of the oribatid species collected in the uncut forest control were rare, representing <1% each of the total oribatid fauna collected. Loss of primary habitat by harvesting whole trees and removing forest floor reduced the number of rare species by half and increased the proportion of species with a

relative abundance >1% from 19% in the uncut forest control to 100% in whole tree/forest floor removal plots. The loss of 'rare' species reduced the diversity and evenness of the oribatid assemblage as treatment severity increased.

Overall, Oppiella nova was the most abundant oribatid mite species in this study and numerically dominant in uncut forest control plots and in all but two treatment plots. This species is parthenogenetic and has a long life span. Coupled with high fecundity and diverse feeding habits, O. nova is able to rapidly occupy a diverse range of habitats in large numbers (Ryabinin and Pan'kov 1987).

Soil pore size can restrict faunal movement and influence relative abundance and species composition (Whitford 1996). Small-bodied mites such as O. nova and Quadroppia quadricarinata (Micheal, 1885) and members of the genera Scheloribates and Suctobelbella are able to use the smaller pore spaces resulting from compaction. Larger species such as Ceratozetes cuspidatus Jacot 1939 and Nothrus borussicus Sellnick 1929 would have difficulty moving through soils with higher bulk densities (Wallwork 1983). Thus, greater densities or proportions of species from families with taxa of small physical size such as Brachychthoniidae, Tectocepheidae and Oppiidae can indicate a recent disturbance (Behan-Pelletier 1999).

Overall, I found that soil compaction and organic matter removal significantly reduced the density and diversity of soil mesofauna in the short-term. Although lower densities may not be permanent, changes to the overall structure may be long lasting (Marshall 1998). For example, oribatid densities

remained at less than 50% of control values seven years after clearcutting in Norway spruce stands in Finland (Huhta 1976). The oribatid assemblage in my study showed a substantial decrease in density and diversity, while maintaining the same dominant species on all treatment plots. The most striking aspect of the response was the loss of rare oribatid species from the treatment plots. If soil mesofauna of sub-boreal forests behave similarly to other studies cited previously, I predict a continued decline in mesofauna density without significant change in the pattern of relative abundance over the first five years after treatment. I expect faunal densities and community structure to recover more slowly on plots where the forest floor has been removed than those where the forest floor remained. Furthermore, since oribatid mites are poor dispersers (Siepel 1996), I expect oribatid density and species diversity to remain low and be dominated by small, parthenogenetic species, such as Oppiella nova.

It is essential to establish baseline data on the density, diversity and structure of the soil fauna assemblage against which to compare changes in recovery of the soil fauna (Behan-Pelletier 1999, Linden et al. 1994). The long-term nature of the LTSPS provides an opportunity to monitor the recovery of the soil fauna community in the SBS over the full rotation period of 80-120 years. This biological data can be integrated with other monitored soil properties, both physical and chemical, to measure the overall response of the forest soil ecosystem to disturbance.

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5.7 Appendices

Appendix A: Equations

Evenness calculation (Hill 1973, Ludwig and Reynolds 1988):

$$E = \frac{N_2-1}{N_1-1}$$

E approaches 0 as a single species becomes more dominant in a community.

Exponential form of Shannon-Wienner function (Hill 1973):

$N_1 = e^{H'}$

where e=2.71828

H' = Shannon-Wienner function (calculated with base e log (LN))

N_1 = number of equally common species which would produce the same diversity as H'.

Shannon-Wienner Function (Magurran 1988):

$H' = -\Sigma\, p_i \ln p_i$

where p_i = the proportional abundance of the i^{th} species.

Reciprocal of Simpson's Index (Hill 1973, Magurran 1988):

$N_2 = 1/D$

where $D = \Sigma \frac{(n_i (n_i -1))}{(N(N-1))}$

where n_i = the number of individuals in the i^{th} species, and N = the total number of individuals.

The value of this index increases with increasing diversity.

Appendix B. Total number of individuals per sample for each oribatid species collected from the organic horizon/mineral soil by each season for each treatment (sites pooled, n=9).

		OM0-C0				OM1-C0				OM3-C0				OM2-C1				OM1-C2				OM3-C2			
		spring	summer	fall	Total	spring	summer	fall	Total	spring	summer	fall	Total	spring	summer	fall	Total	spring	summer	fall	Total	spring	summer	fall	Total
PALAEOSOMATA																									
Palaeacaridae																									
Palaeacarus hystricinus	Tragardh, 1932	0/1	0/2		0/3											1/0	1/0								
ENARTHRONOTA																									
Atopochthoniidae																									
Atopochthonius arboctactylus	Grandjean, 1948	1/0	0/1	0/1	1/2										1/0		1/0								
Brachychthoniidae																									
Brachychthonius bimaculatus	Willmann,1936	0/1			0/1																				
sp.		0/1			0/1																				
Liochthonius brevis	(Michael, 1888)			2/0	2/0															1/0	1/0				
lapponicus	(Tragardh, 1910)																			2/0	2/0				
sueconum	Forsslund, 1964		1/0		1/0		2/0	2/0	4/0					1/0	1/0	2/0	4/0	5/2		1/0	6/2				
simplex	(Forsslund, 1942)		0/1		0/1		1/0	1/0	2/0																
lunare	Forsslund, 1957	1/0			1/0																				
sp.		1/0	4/0	7/0	12/0		1/0	2/0	3/0		0/1		0/1	1/0			1/0								
Neoliochthonius sp.nr. globuliferus								1/0	1/0																
Sellnickochthonius immaculatus	(Forsslund, 1942)			3/0	3/0							0/1	0/1												
suecica	Forsslund, 1942			6/0	6/0		2/0		2/0			0/1	0/1		0/1	1/0	1/1		0/1		0/1				
sp.nr. suecia		2/4			2/4																				
Synchthonius crenulatus	(Jacot, 1938)	0/1			0/1		0/1		0/1						1/0		1/0								
elegans	Forsslund, 1957					1/1		1/0	2/1																
Vesichthonius sp.		13/0			13/0																				
Pterochthoniidae																									
Pterochthonius angelus	(Berlese,1910)	1/0	1/0	6/1	8/1			2/0	2/0						1/0	1/0	2/0	1/0			1/0				
MESONOMATA																									
Euphthiracaridae																									
Euphthiracarus cernuus	Walker, 1965	1/0	1/0	2/0	4/0	1/0			1/0					3/1	1/0		4/1	1/0		3/0	4/0				
Oribatellidae																									
Protoribotritia sp.		1/0			1/0		1/0		1/0					1/0			1/0	2/0	0/1	1/0	3/1				
Phthiracaridae																									
Phthiracarus longulus	(C.L. Koch, 1841)					1/0			1/0																
brysbus	Jacot, 1931			1/0	1/0	2/0			2/0										1/0		1/0				
DESMONOMATA																									
Camisiidae																									
Camisia lapponica	(Tagadh, 1910)	1/0			1/0																				
spinifer	(C.L. Koch, 1835)	0/1			0/1																				
Heminothrus longisetosus	Willman, 1925	17/0	25/0	9/0	51/0	1/0	2/0	4/0	7/0					7/0	1/0	8/1	16/1	1/0	7/0	1/0	9/0				
Nanothrus humicola	(Forsslund, 1955)	2/1	2/0	1/0	5/1	1/0			1/0	0/1			0/1					0/2	0/6	1/0	1/8				
Platynothrus peltifer	(C.L. Koch, 1893)	2/1	3/0	2/0	7/1															1/0	1/0	0/1		0/1	
septentrionalis	(Selinck, 1944)			1/0	1/0			1/0	1/0							1/0	1/0								
sp.nr.		2/0	1/0	4/0	7/0																				

		OM0-C0				OM1-C0				OM3-C0				OM2-C1				OM1-C2				OM3-C2			
		spring	summer	fall	Total	spring	summer	fall	Total	spring	summer	fall	Total	spring	summer	fall	Total	spring	summer	fall	Total	spring	summer	fall	Total
Appendix B continued																									
Nothridae																									
Nothrus																									
anauniensis	Canestrini et Fanzago, 1876		2/0		2/0																				
borussicus	Sellnick, 1929	1/0		14/0	15/0	5/0	1/0	30/0	36/0					3/0		26	29		1/0	13/0	14/0				
silvestris	Nicolet, 1855															1/0	1/0								
sp.nr. pluchellus			0/1		0/1																				
Trhypochthoniidae																									
Trhypochthonius																									
tectorum	(Berlese, 1896)													2/0	1/0		3/0								
BRACHYPYLINA																									
Astegistidae																									
Cultroribula																									
bicultrata	(Berlese, 1905)														1/1		1/1								
Cepheidae																									
Cepheus																									
cornu	Jacot, 1928	1/0			1/0																				
Ceratozetidae																									
Ceratozetes																									
cuspidatus	Jacot,1939	3/0	16/1	11/1	30/2	7/0	17/2	1/1	25/3					3/0	1/0	5/0	9/0			1/0	1/0				
thienemanni	Willmann	20/13	9/0	4/5	33/18	53/3	23/6	2/11	78/20					1/0	3/2	9/0	13/2	0/1	12/30	4/5	16/36				
pacificus	Behan-Pelletier, 1984							2/0	2/0																
Denizetes																									
ruderiger	Hammer, 1952					1/0		1/0	2/0										1/0		1/0				
Hexozetes																									
lutzus	(Hammer, 1958)		1/0	1/0	2/0			2/0	2/0																
Sphaerozetes																									
sp.															1/0		1/0								
Trichorbates																									
coopermineusis	Hammer, 1952																							0/1	0/1
Damaeidae																									
Belba																									
sp.				1/0	1/0											1/0	1/0			3/0	3/0				
Epidamaeus																									
articulus	(Hammer, 1952)													1/0			1/0								
konyukon	Behan-Pelletier and Norton, 1985					4/0		1/0	5/0																
sp.nr. corallo		1/0	5/0		6/0	1/0	2/0		3/0			0/1	0/1	1/0	1/0		2/0		2/0		2/0	0/1			0/1
sp.nr. floccosus																1/0	1/0								
sp.nr. kodiakensis			1/0	4/0	5/0		0/1		0/1	0/1			0/1					1/0			1/0				
Eremaeidae																									
Eremaeus																									
brevilarus	(Ewing, 1917)	15/1	3/0	1/0	19/1	1/0	4/0	6/0	11/0		0/1	0/1	0/2	2/0	4/0	6/0	12		6/0	1/1	16/1			0/1	0/1
translamellatus	Hammer, 1952	7/0		3/1	10/1	2/0	2/0		4/0									1/0	2/0		3/0				
Eueremaeus																									
sp.nr. marshalli			1/0		1/0																				
Galumnidae																									
Pilogalumna																									
sp.nr. tenuidens		1/0			1/0	1/0	3/0		4/0							1/0	1/0	1/0		1/0	2/0				
Gymnodamaeidae																									
Gymnodamaeus																									
sp.nr. bicaudatus	Paschoal, 1982	3/0	5/0	2/0	10/0			1/0	1/0									2/0	1/0		3/0				
Hermanniellidae																									
Hermanniella																									
picea	(C.L. Koch, 1839)																			3/0	3/0				
Liacaridae																									
Liacarus																									
bidentatus	Ewing, 1918		1/0		1/0							0/1	0/1												
Metrioppidae																									
Ceratoppia																									
quadridentata	Hammer, 1955		2/0		2/0																				

		OM0-C0				OM1-C0				OM3-C0				OM2-C1				OM1-C2				OM3-C2			
		spring	summer	fall	Total	spring	summer	fall	Total	spring	summer	fall	Total	spring	summer	fall	Total	spring	summer	fall	Total	spring	summer	fall	Total
Appendix B continued																									
Mycobatidae																									
Mycobates incurvatus	Hammer, 1952		1/0	1/0	2/0			5/0	5/0																
punctatus	Hammer, 1955			1/0	1/0																				
Oppiidae																									
Lauroppia sp.											0/4		0/4		7/0		7/0								
Muritoppia claviger	(Hammer, 1952)	42/29	16/5	0/114	58/148	17/30	8/8	0/1	25/39	0/3	0/1		0/4	4/0	3/4	1/0	8/4	13/10	5/17	0/2	18/29	0/1			0/1
Multioppia sp.				1/0	1/0			4/0	4/0						1/0		1/0	1/0		1/0	2/0				
Oppia sp.1		11/0	4/0	10/0	25/0																				
Oppiella nova	(Oudemans, 1902)	447/30	194/18	278/223	919/271	279/76	147/72	4/19	466/167	0/8	0/12	0/12	0/32	156/13	17/5	54/2	227/20	7/15	52/5	28/7	87/27	0/79	0/1		0/2 0/82
wasbluni	(Hammer, 1952)			19/9	19/9			1/5	1/5			0/4	0/4		6/0		6/0			2/0	2/0				
Quadroppia quadricarinata	(Michael, 1885)	16/1	6/0	5/3	27/4	17/4	25/0	51/0	93/4					11/0	6/0	8/0	25/0	4/0	6/0	21/1	31/1	0/2			0/2
Oribatulidae																									
Jomada n.sp.			4/0	9/0	13/0	2/0	7/0	12/3	21/3					1/0	1/0	0/3	2/3								
Oribatula tibialis	(Nicolet, 1855)	8/0	4/0	7/0	19/0	20/0	14/0	28/1	62/1			0/1	0/1	6/1	16/0	46/4	68/5	12/0	8/0	17/3	37/3			0/2	0/2
Phenopelopidae																									
Eupelops sp.nr. plicatus		2/0	0/1	1/0	3/1			1/0	1/0																
Polypteroxeniidae																									
Polypterozetes sp.																			1/0	5/0	6/0				
Scheloribatidae																									
Scheloribates pallidulus	(C.L. Koch, 1841)																			1/0	1/0				
sp.1		13/1	1/0	10/18	24/19	6/1	16/3	1/0	23/4					1/0	1/0	2/0	4/0	1/6			1/6				
Suctobelbidae																									
Suctobelba sp. 1		1/0	2/0	3/0	6/0	1/0	2/0		3/0					1/0			1/0			1/0	1/0				
sp.2			1/0		1/0		1/0		1/0					1/0			1/0								
Suctobelbella sp.nr. equidens		48/14	81/8	55/5	184/27	54/16	48/6	15/16	117/38	0/11		0/2	0/13	75/7	17/5	2/4	112/16	13/5	19/12	22/7	54/24	0/1			0/1
sp.nr. subcornigera			2/0		2/0		1/0		1/0																
sp. 2		13/0	9/4	6/2	28/6	16/2	13/2	8/15	37/19	0/1			0/1	1/1	4/0	5/0	19/1	2/0	4/0	3/0	9/0	0/4			0/4
sp. 3		5/0	0/1	24/2	29/3		6/0	1/8	7/8			0/1	0/1	22/0	6/0	3/4	31/4		1/0	8/0	9/0	0/4			0/4
sp. 4		2/1			2/1		1/0		1/0						1/0		1/0								
sp. 5			2/0		2/0									1/0			1/0		1/0		1/0				
sp. 6			16/0	13/6	29/6	1/0	22/1	3/8	26/9	0/2		0/1	0/3	1/0	7/1	15/1	23/2		7/0	13/0	2/0	0/5			0/5
sp. 7		2/2		0/2	2/4	0/1	0/2	2/0	2/3						1/0		1/0								
sp. 8		0/1			0/1	2/2		0/1	2/3							17/1	17/1			1/0	1/0				
sp. 9				3/0	3/0		6/0		6/0							1/0	1/0			3/0	3/0				
sp. 10																2/0	2/0			1/0	1/0				
Tectocephidae																									
Tectocepheus velatus	(Michael, 1880)	3/1	8/0	1/0	14/1	9/0	14/6	15/0	38/6	0/2		0/1	0/3	6/0	2/2	2/0	10/2	4/0	7/0	1/0	12/0				
Undetermined sp.1		1/0			1/0									1/0			1/0								
Undetermined juveniles		58/13	48/0	63/4	169/17	9/24	56/8	18/32	83/64	0/1	0/10	0/4	0/15	5/0	24/3	27/2	56/5	0/1	3/50	5/7	8/58		0/1	0/1	0/2

Chapter 6: General Conclusions

6.1 Differences among sites

Knowledge of the density, diversity and structure of the soil fauna community in most geographical regions and in different ecosystems is limited (Marshall 1998). Surveys of soil fauna in different regions and ecosystems provide the basis for comparative studies and for examining the response of soil fauna to environmental disturbances. In the present study, densities and relative abundance of several groups of soil fauna differed significantly among sites even though most classes and orders of soil organisms are widely distributed (Anderson 1977). For example, densities of predatory groups, such as spiders, pseudoscorpions, centipedes, and ants differed among sites. High spider and low ant densities were observed at both Topley and Skulow Lake while a high density of ants, increased densities of pseudoscorpions and centipedes and low density of spiders were observed at Log Lake. Ants can exert a strong influence on ecosystem function (Kajak et al. 1972) and their foraging activity may influence spider density (Petal and Breymeyer 1969). Predation also reduces densities of prey groups, altering the structure of the soil fauna community and possibly leading to local extinction of certain prey species (Giller 1996).

Density and diversity of earthworms also differed among sites. Density of earthworms was higher at Log Lake while species richness was greater at Skulow Lake. Dendrobaena octaedra (Savigny) was collected at all threes sites but Lumbricus rubellus Hoffmeister was collected only at Skulow Lake. Since

earthworm activity affects both soil chemical and physical properties, their presence would also impact on the diversity and density of the soil fauna community (Loranger et al. 1998, Giller 1996). The presence of L. rubellus at Skulow Lake may have contributed to the differences in humus forms and soil chemical and physical properties among the sites due to its larger size than D. octaedra (Reynolds 1977). The humus form at Skulow Lake is considered a moder-type while those at Topley and Log Lake have been classified as hemimor humus forms. Huhta et al. (1967) suggested that L. rubellus contributed to moder humus formation at one study site in Finnish forest soils.

Earthworm casts totally replaced upper organic horizons in Pinus contorta forests of southwestern Alberta (MacLean et al. 1996) and in virgin podzol soils of Atlantic Canada (Langmaid 1964). Increased amounts of fecal material, with a higher pH, can also counteract acid conditions found in mor humus forms (Wallwork, 1970). As pH increases, both soil microbial and faunal communities change. Bacterial biomass would increase while fungal biomass would decrease in conjunction with an increased dominance of macrofauna and a reduced mesofauna component as well as an increased abundance of bacterial feeding organisms (Wallwork 1970, Schaeffer and Schauermann 1990).

Densities and relative abundances of oribatid mites also differed significantly among sites. In the present study, both density and relative abundance of oribatid mites were similar between Topley and Skulow Lake (approximately 60,000/m^2 and 35%, respectively). At Log Lake however, density and relative abundance of Oribatida were significantly lower (30,000/m^2 and

23%, respectively). This difference among sites suggests a previous disturbance to the soil ecosystem at the Log Lake site. Oribatid mites take a long time to recover from disturbances. For example, 15 years after tree harvest in a spruce forest in Finland, oribatid populations remained at 50% of control populations while prostigmatid populations returned to near control values (Huhta and Koskenniemi 1975).

Diversity values of both N_1 and N_2 were lower for the organic horizon at Log Lake than either Topley or Skulow Lake. Oppiella nova was abundant at Log Lake, representing nearly 70% of the oribatid fauna. Greater densities or proportions of species from families such as Brachychthoniidae, Tectocepheidae and Oppiidae, to which O. nova belongs, can indicate a recent disturbance (Behan-Pelletier 1999).

Assemblages of oribatid mite species were similar among sites. Similarity in oribatid species assemblages of the organic horizons was near 93% among all three sites. However, in the mineral soil, Log Lake and Skulow Lake were more similar to each other (86%) than to Topley (40%). Differences in similarity among sites reflect the different species dominant in the mineral soil. O. nova was numerically dominant for all seasons, sites and horizons except in the mineral soil at Topley that was dominated by Moritzoppia clavigera.

Eighty-nine oribatid mite species were identified in this study, more than double the number of oribatid species previously recorded in British Columbia (Behan-Pelletier 1993). Furthermore, 11 species were recorded for the first time in Canada. The majority of described oribatid species identified in this study are

broadly distributed in the Northern Hemisphere (65% were Holarctic and 29% were Nearctic). The wide northern distribution of these species combined with reliable taxonomical surveys of oribatid mite species from northern European forests allows for greater resolution of identified species (Behan-Pelletier 1999).

Soil ecosystems at these sites are complex with high densities and species diversity. The long-term impact of increased earthworm activity on the structure of the soil fauna community as well as changes to various soil chemical and physical properties, nutrient cycling and decomposition rates in these coniferous forests are unknown at this time but deserve further study. Structure of the soil fauna community, even when identified at the family and order level, can indicate differences among sites due to climatic, physical and chemical soil properties or disturbed habitats. Differences in the macrofauna community were limited to earthworms and proportions of spiders, centipedes, ants and pseudoscorpions. Analysis using higher taxa gives a more conservative interpretation of results (Haskell 2000). If an effect is significant at this level, a more severe impact is probable at the species level. Loss of species can occur without affecting the overall density of the higher taxa. This can provide a starting point and a baseline collection for further exploration in differences and similarities among different sites and for different types or levels of habitat disturbance. More surveys of soil fauna identified at this level are required to establish the basis for comparisons among sites or disturbances. Although knowledge of ecology and life history of most species of soil organisms is limited at present, continued collection of ecological and biological data on community

structure and species diversity in soil ecosystems will indicate soil health and potentially aid in the identification of the type of site disturbance (Behan-Pelletier 1999).

6.2 Impact of organic matter removal and soil compaction

Overall, stem only harvesting with no compaction did not significantly alter the density and structure of the soil fauna community compared to the uncut forest control. However, whole-tree harvesting combined with light compaction or stem only harvesting with heavy compaction reduced densities of most soil fauna taxa by more than 50% of control values after one year. These results were similar to reductions in faunal densities observed by other studies (Huhta et al. 1967, Bird and Chatarpaul 1986, Blair and Crossley 1988). Removal of the forest floor significantly reduced density and diversity of the soil fauna community since more than 80% of the soil fauna reside in this horizon (Wallwork 1970). The construction of skid trails, logging roads, landings and sorting decks as well as site preparation practices such as scarification that result in a total removal of the organic horizon would be detrimental to soil fauna populations.

Although densities of soil macrofauna decreased with harvesting and compaction, relative abundance for most macrofauna taxa remained unchanged. Huhta et al. (1967) also reported no conspicuous changes in relative abundance among macrofauna after clear-cutting. This indicates that, in the short-term, whole tree and stem only harvesting combined with soil compaction had little impact on the overall structure of the soil macrofauna community. Another

interpretation could be that the impact of these treatments on soil macrofauna may be delayed and not observable until two to three years after treatment application (David et al. 1991).

The coarseness of identification of macrofauna provided a conservative indication of disturbance since changes in species richness could occur without affecting the density of classes or orders (Haskell 2000). Although species level identification would be ideal, there is a limited window of opportunity to collect and process this preliminary data. Now that samples are collected and available, further study at the species level can be carried out, provided there is interest and financial support.

Soil mesofauna did not respond in the same manner as macrofauna in the present study. Density of soil mesofauna decreased and the structure of the mesofaunal community also changed. For example, both density and relative abundance of oribatid mites declined significantly as treatment severity increased. While densities of Mesostigmata and Prostigmata also decreased, relative abundance of both taxa increased as treatment severity increased. Oribatid mites were more sensitive to changes in their environment and decreased in number at a greater rate than Prostigmata or Mesostigmata. Because of their rapid decline in both density and diversity in disturbed habitats, oribatid mites may be useful biological indicators (Behan-Pelletier 1999).

Declines in oribatid diversity and density after harvesting have been related to the loss or delayed development of fungi in organic matter (Huhta et al. 1967). Generally, fungi dominate most forest soils and bacteria are prominent in

agricultural soils (Wallwork 1970), and most mites and springtails in forest soils feed on this fungal biomass. However, tree harvesting and soil compaction can increase bacterial diversity and biomass in forest soils (Marshall 1998), thereby altering food resources available to soil mesofauna. An increase in bacterial biomass could influence the density of microbial feeding species, such as members of the oribatid mite family Suctobelbidae (Ryabinin and Pan'kov 1987), altering the overall structure of the mesofaunal assemblage.

Some oribatid species avoid colder temperatures and drought conditions by moving deeper into the soil profile (Wallwork 1970, Siepel 1996). Soil compaction increases bulk density, limiting vertical movement of soil fauna in the soil profile, even for smaller species such as O. nova. In the present study, bulk density of the mineral soil was significantly higher in both light and heavy compaction plots than in those plots with no compaction (see Chapter 2, Kranabetter and Chapman 1999). Densities of soil mesofauna in mineral soil still covered by forest floor were higher than in mineral soil where forest floor had been removed. The forest floor may act as a buffer, reducing the degree of compaction (Donnelly and Shane 1986) and thus limiting increases in bulk density and temperature fluctuations.

In the present study, tree harvesting and forest floor removal reduced oribatid mite diversity and species richness and changed the structure of the oribatid mite species assemblage. The loss of 'rare' species from the treatment plots was the most remarkable aspect of the response. Diversity and evenness of the oribatid assemblage declined as treatment severity increased. The

proportion of rare species, those with <1% relative abundance, decreased by half while the proportion of common species increased five fold. Bird and Chatarpaul (1986) also found the relative abundance of several oribatid taxa differed significantly after harvesting but observed no change in the taxa present. In contrast, Siepel (1996) concluded that forest harvesting did reduce the number of oribatid species.

Oppiella nova was the most abundant oribatid mite species in this study and numerically dominant in the uncut forest control plots and in all but two treatment plots. This species is parthenogenetic and has a long life span. Coupled with high fecundity and diverse feeding habits, O. nova is able to rapidly recolonize disturbed habitats in large numbers (Ryabinin and Pan'kov 1987). Continued species level work examining life history and ecological roles of species in the soil ecosystem may even help to determine the type of disturbance to the soil habitat (Behan-Pelletier 1999).

Although lower densities may not be permanent, changes to the overall structure may be long lasting (Marshall 1998). The length of time required for the diversity and density of soil fauna communities to recover to pre-disturbance levels is unknown and may take longer than intended rotation periods. Bird and Chatarpaul (1986) suggested that faunal densities could take from 10-13 years to return to pre-harvest levels. For example, densities of oribatid mites remained at <50% of control values 15 years after clearcutting in Norway spruce stands in Finland (Huhta and Koskenniemi 1975).

The establishment of baseline information on the density, diversity and structure of the soil fauna community is essential for future comparisons (Behan-Pelletier 1999, Linden et al. 1994). Continued monitoring of the LTSP sites for the duration of the study will provide valuable information on long-term responses to and recovery of soil fauna from soil compaction and organic matter removal. Biological data can be integrated with other monitored soil properties, both physical and chemical, to examine long term soil productivity of the forest soil ecosystem in the SBS in response to disturbance. This knowledge will aid in development of guidelines for ecologically beneficial harvesting practices to enhance long-term sustainability of forest soils.

Basic recommendations from this study are simple and straightforward. Since >80% of soil organisms dwell in the organic horizon, disturbance or removal of this horizon should be kept to a minimum. Organic matter provides food and shelter to the organisms residing in this layer as well as nutrients for tree growth. Furthermore, site rehabilitation and the re-establishment of an organic layer on areas such as logging roads, skid trails, landings and sorting decks should be considered as well in order to re-establish a functioning soil ecosystem on these disturbed areas. It may be possible to store the organic matter removed during construction and re-spread it once harvesting is completed in an area. Soil compaction should also be kept to a minimum since it alters physical and biological properties in the soil ecosystem. The incorporation of organic matter back into mineral soil would help limit soil compaction and aid in the development of the soil ecosystem.

These recommendations deal specifically with short-term response of soil fauna to soil compaction and organic matter removal. By limiting short-term reduction in densities and diversity and maintaining the integrity of the soil fauna community, long-term productivity in forest soils should be enhanced.

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